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Diversified agroecosystems for biodiversity and ecosystem services

Ecological intensification of faba bean cropping under
land use and climate change

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Cover: Faba bean field in a diverse agricultural landscape and its pollinators and pest insects.

(illustrations: Chloë Raderschall, photographs: Oskar Renstamm Rubbmark (aerial) and Chloë Raderschall (faba bean with buckwheat))

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Abstract

Loss of natural habitats and lack of continuous floral resources in intensive agricultural landscapes limit the population growth of ecosystem service providers, such as pollinators. Weakened ecosystem service delivery and climate change stressors contribute to crop yield instability. The aim of my thesis was to explore how resource diversification strategies at both field and landscape scale influence arthropod communities and the services they provide, such as pollination and biological pest control. Further, I explored how climate change stressors such as water stress and insect herbivory interact with insect pollination and affect crop yield. To address these aims, I used faba bean cropping as a model system. I found that landscape crop diversity enhanced bumble bee densities and flower strips enhanced ground predators in the crop. Flower strips boosted and honey bee hives counteracted bumble bee queen abundances in the landscape across seasons. Using pollinator exclusion experiments, I showed that insect pollination increased yield. This insect pollination benefit decreased with increasing semi-natural habitat cover in the landscape but was constant irrespective of plant water stress and insect herbivory. I demonstrated that the highest yields are achieved when water stress and insect herbivory are reduced simultaneously. My thesis emphasises that diversified agroecosystems are particularly important in the face of climate change, because they 1) enhance ground predators that can safeguard crops from herbivore outbreaks, and 2) provide pollinators with floral resource continuity, which arguably is particularly important during extremely hot and dry summers, where landscape-wide floral resource bottlenecks are worsened by shortened bloom periods.

Keywords: crop diversity, flower strips, pollination, biological pest control, bumble bees, sustainable agriculture

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Diversifierade agroekosystem för biologisk mångfald och ekosystemtjänster

Sammanfattning

Förlust och fragmentering av naturliga livsmiljöer och brist på kontinuerlig tillgång till blomresurser i intensivt odlad åkermark begränsar populationstillväxten hos ekosystemtjänstleverantörer, som pollinerare. Försvagad leverans av ekosystemtjänster och stressfaktorer till följd av klimatförändringar bidrar till skördeinstabilitet hos grödorna. Syftet med denna avhandling var att undersöka hur strategier för resursdiversifiering på både fält- och landskapskala påverkar insekter och spindlar och de ekosystemtjänster de tillhandahåller, som pollinering av grödor och biologisk bekämpning av skadeinsekter. Vidare undersökte jag hur klimatförändringsfaktorer som vattenbrist och ökad förekomst av växtätande insekter samverkar med insektpollinering i sin skördepåverkan. För att undersöka dessa frågor har jag använt odling av åkerböna som modellsystem. Jag fann att en mångfald av grödor i landskapet ökade mängden humlor och blomremсор gynnade marklevande naturliga fiender som spindlar och jordlöpare i åkerbönfälten. Blomremсор gynnade och honungsbisamhällen motverkade mängden övervintrade humledrottningar i landskapet. Genom experiment som uteslöt pollinerare visade jag att insektpollinering ökade skörden. Skördeökningen till följd av insektpollinering var oberoende av om åkerböna led av vattenbrist eller angrepp av växtätare men minskade med mängden naturliga livsmiljöer i landskapet. Jag visade att de högsta skördarna uppnås när både vattenbrist och växtätande insekter minskas samtidigt. Min avhandling understryker att diversifierade agroekosystem är särskilt viktiga i ljuset av klimatförändringar eftersom de 1) gynnar marklevande naturliga fiender som kan skydda grödorna mot angrepp av växtätande insekter och 2) ger pollinerare blomresurskontinuitet, vilket kan vara särskilt viktigt under extremt varma och torra somrar när flaskhalsar i blomresurstillgången förvärras av förkortade blomningstider.

Nyckelord: mångfald av grödor, blomremсор, pollinering, humlor, biologisk bekämpning av skadegörare, hållbar jordbruk

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Dedication

To all the current and future PhD students who doubt themselves. You can do it!

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List of publications

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

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- II. Raderschall, C.A., Lundin, O., Lindström, S.A.M., Bommarco, R. Annual flower strips and honeybee hive supplementation differently affect arthropod guilds and ecosystem services in a mass-flowering crop (manuscript)
- III. Bommarco, R., Lindström, S.A.M., Raderschall, C.A., Gagic, V., Lundin, O. Flower strips enhance bumble bee abundance across seasons in landscapes with few honey bee hives (submitted manuscript)
- IV. Raderschall, C.A., Vico, G., Lundin, O., Taylor, A.R., Bommarco, R. (2021). Water stress and insect herbivory interactively reduce crop yield while the insect pollination benefit is conserved, *Global Change Biology*, 27: 71-83

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The contribution of Chloë Aline Raderschall to the papers included in this thesis was as follows:

- I. Main author. Participated in the development of the research questions and sampling design. Supervised and conducted the field work. Analysed the data, interpreted the results and wrote the manuscript with help from RB and OL.
- II. Main author. Participated in the planning of the sampling methodology. Supervised and conducted the field work with some advice from co-authors. Analysed the data, interpreted the results and wrote the manuscript with some assistance from RB and OL.
- III. Co-author. Participated in the idea formation and the development of the sampling design. Conducted the landscape analysis. Co-supervised the field work, which was led by SAML. Participated in the interpretation of results. Contributed to the writing of the manuscript, which was led by RB.
- IV. Main author. Conceived the project idea and planned the experiment together with GV, OL and RB. Supervised and conducted the field work. Analysed the data, interpreted the results and wrote the manuscript with assistance from all co-authors.

Abbreviations

EFN	Extra floral nectaries
EU	European Union
FAO	Food and Agriculture Organisation of the United Nations
GIS	Geographic information system
SNH	Semi-natural habitats, i.e. forests and pastures

1. Introduction

How do we manage agricultural landscapes in the future to feed an increasingly wealthy human population that is undergoing major diet changes, without concurrently compromising environmental health, biodiversity and the stability of ecosystem functions? This question gets to the heart of one of the greatest global challenges we are currently facing (Rockström et al., 2017).

The industrialisation of agriculture has succeeded in dramatically increasing the amount of food that is produced per unit of land (Godfray et al., 2010). The paradigm of industrial agriculture has its cradle at the onset of the Green Revolution, which is characterised by vast monocultures of few high-yielding crop varieties, use of agrochemicals to fertilise crops and control pests and heavy mechanisation to work the fields more efficiently (Pingali, 2012). In the shadow of this apparent progress lies an unprecedented loss of biological diversity – often referred to as the sixth mass extinction on Earth (Ceballos et al., 2020; IPBES, 2019). With every species or population that disappears, ecological interactions are eroded and important ecosystem functions, such as pollination, lost.

Climate change is further modifying agroecosystems and species interactions that impede crop production. For example, rising temperatures increase herbivory in plants as a result of expanding species distributions, increased herbivore consumption rates, and reduced resistance in plants (Hamann et al., 2021; Lehmann et al., 2020). Agricultural systems, which provide fewer host plant options than natural systems, are particularly prone to increased herbivore consumption rates (Hamann et al., 2021). In addition, more frequently occurring extreme weather events, such as prolonged heat and dry periods associated with climate change are causing major crop yield losses (Seneviratne et al., 2012).

Degraded ecosystem functions due to land use changes and more frequent insect pest outbreaks, heat or water stress associated to climate change, are among the major contributors that increase yield instability and threaten food security (Seneviratne et al., 2012). To halt this dire prognosis, we need to reduce harmful agrochemical inputs and instead strengthen agricultural production by fostering ecosystem functions (Bommarco et al., 2013) that bolster crop production and are robust against environmental perturbations (Redhead et al., 2020). Arthropods fulfil particularly important functions in agroecosystems, such as pest suppression, pollination and nutrient cycling (Losey and Vaughan, 2006). For such ecological intensification to be successful, we need a comprehensive understanding of how land use changes at different scales affect arthropod communities, their interactions and ecosystem functions, and how these functions are influenced by climate change stressors.

1.1 Biodiversity and ecosystem services

Biological diversity, hereafter biodiversity, encompasses the variety among living organisms in terms of their genes, species or functional traits (Cardinale et al., 2012). Biodiversity is commonly quantified as richness, which is a measure of the number of unique species and evenness, which is a measure of equitability among species. Together, richness and evenness quantify the heterogeneity among life forms (Cardinale et al., 2012). Biodiversity is fundamental to the evolution of natural ecosystems and the conservation of their functions, of which a subset provide important services for human societies and are therefore collectively referred to as ecosystem services (Altieri, 1999; MA, 2005).

Within the agricultural context, arthropods are important ecosystem service providers (Losey and Vaughan, 2006). Bees visit and pollinate flowers, ladybird beetles and other predators control many pests, and dung beetles decompose waste and so improve nutrient cycling (Losey and Vaughan, 2006), yet all of these interactions are susceptible to human actions such as land use change (Bengtsson, 2010). During their life cycle, arthropods need to disperse among similar habitat patches in the landscape to find foraging resources, shelter or overwintering sites - or disperse to find a mate, reproduce and start a new population (Gounand et al., 2018). The size of populations is limited, among other factors, by resource

discontinuity (Schellhorn et al., 2015). Meta-community theory explores how a set of spatially distinct populations nested within a landscape are linked with each other by dispersal of multiple potentially interacting species (Leibold et al., 2004). The theory predicts that landscape heterogeneity, connectivity among habitat patches, and resource continuity are essential for populations to persist, to promote species diversity and maintain ecosystem services (Bengtsson, 2010). In contrast, homogeneous landscapes, which lack resource continuity and connectivity among similar habitat patches, will harbour lower species diversity and less efficient ecosystem services (Bengtsson, 2010). Ecosystem services in landscapes with poor species diversity are expected to be less resilient against perturbations since they are compromised in some key mechanisms underpinning biodiversity and ecosystem functions such as complementarity, functional redundancy or facilitation (Altieri, 1999; Loreau and de Mazancourt, 2013; Oliver et al., 2015; Tscharrntke et al., 2005; Wright et al., 2017) (Box 1).

Box 1: Biodiversity and ecosystem functions

A biodiverse ecosystem is pivotal to ensure effectiveness and resilience of ecosystem functions in response to perturbations due to a set of mechanisms including:

- 1) **Species complementarity:** Different species complement each other by occupying different niches, thereby using resources more completely and enhancing the ecological functioning. For example, different natural enemies control insect pests in different ways, times or places and so increase overall pest control.
- 2) **Redundancy:** Multiple species share the same functions, which safeguards ecosystems to overcome disturbances. For example, a plant that is visited by multiple pollinators is more likely to survive a disturbance that might drive some pollinators to extinction.
- 3) **Sampling effect:** With higher diversity there is a greater chance of including a key species, which is particularly beneficial for that ecosystem. For example, a certain crop species (red clover) attracts a lot of bumble bees.
- 4) **Facilitation:** The existence of one species favours the existence of a co-occurring species. For example leguminous crops make atmospheric nitrogen available for nearby crops and so enhance their productivity.

1.1.1 Biodiversity in changing agricultural landscapes

In intensively managed agricultural landscapes, extensive fields cultivated with few crop species in monocultures, simple crop rotations and isolated patches of natural habitats have reduced arthropod biodiversity (Raven and Wagner, 2021; Wagner et al., 2021b). In line with meta-community theory mentioned above, crop pollinators and natural enemies of pests need to disperse among crop fields for specific food resources and require nearby natural habitats as nesting and overwintering sites (Öckinger and Smith, 2007; Thies and Tschardtke, 1999). Simplified agricultural landscapes, which lack such habitat connectivity and resource continuity, will select for a small number of species with high dispersal abilities and generalist

resource requirements (Bengtsson, 2010) thereby weakening ecosystem services stability and augmenting the risk of e.g. pest outbreaks (Bennett et al., 2012; Dainese et al., 2019; Matson et al., 1997). As an alternative, diversification of cropping systems opts for an integration of different functionally important plant or crop species that can provide forage resource continuity and aid dispersal among habitats and so enhance biodiversity and ecosystem functions (Gurr et al., 2017; Tiemann et al., 2015). Such diversification measures can be integrated at different temporal scales (i.e. more diverse crop rotation) or at different spatial scales (i.e. local establishment of flower strips or landscape heterogeneity) and are pivotal to sustainable agriculture (Hufnagel et al., 2020; Isbell et al., 2017; Landis, 2017; Malezieux et al., 2009).

Wild bees are important ecosystem service providers and their abundances, diversity and pollination service to crops in relation to land use and climate change have been intensively studied. Bee densities, richness and diversity have steadily declined over recent decades (Zattara and Aizen, 2021) compromising the provision of crop pollination (Duchenne et al., 2020b; Goulson et al., 2015; Grab et al., 2019; Potts et al., 2016). In fact, globally approximately 25% fewer bee species were recorded between 2006 and 2015 than before the 1990s (Zattara and Aizen, 2021). The conversion of natural habitats into agricultural fields and the associated loss of continued and diverse floral resources and nesting habitats are the major drivers limiting bee populations (Goulson et al., 2015; Schellhorn et al., 2015). In addition, increasing temperature due to climate change advances bee foraging activity on average by six days and shortens their activity period by two days in Europe (Duchenne et al., 2020a). However, not all bees and other insect species are negatively affected by global change drivers. Populations of certain species also respond positively or do not respond at all to agricultural intensification and climate change (Biesmeijer et al., 2006; Bommarco et al., 2012; Duchenne et al., 2020b; Shackelford et al., 2013; Wagner et al., 2021a). Among bumble bee species, for example, which are pivotal crop pollinators in temperate agriculture, the generalist species increased in abundance in response to agricultural intensification while more specialised species starkly declined or even went extinct (Bommarco et al., 2012). Such shifts in pollinator assemblages are compromising the resilience and stability of crop pollination.

1.1.2 Ecosystem services

Agricultural crop production is supported by a set of ecosystem services, which according to the Millennium Ecosystem Assessment are defined as the benefits of ecosystem functions to human societies and grouped into four categories (MA, 2005) (Box 2). While the Millennium Ecosystem Assessment definition provided a good starting point to assign human value to ecological processes, the paradigm has since been further developed and refined to emphasise the cascading relationship among intermediate ecosystem services (i.e. pollination and biological pest control) that eventually conclude into final ecosystem services (i.e. crop yield) comprising goods and values to humans (Mace et al., 2012).

Box 2: Ecosystem services

Ecosystem services encompass functions provided by ecosystems that benefit us, as a society (MA, 2005). The types of services are grouped into four categories:

- 1) **Provisioning services**, such as food, fibre, fuel, water and timber.
- 2) **Regulating services**, such as pest and disease control, pollination, climate regulation and water purification.
- 3) **Supporting services**, include soil formation, photosynthesis and nutrient cycling.
- 4) **Cultural services**, provide recreational resources, aesthetic value.

Insect pollination of crops

Pollination is the process by which pollen gets transferred from the male to the female flower parts – the stigma – and enables the reproduction of plants (Potts et al., 2016). Pollination between plant individuals is referred to as cross-pollination, while pollination within a single plant is called self-pollination. Since plants are sedentary, the pollen transfer between plants is

vectored by either wind, water or animals. Cross-pollination by animals (pollinators), enhances both seed or fruit quantity and quality of about 75% of the 115 major crop species accounting for about 35% of the global food production (Klein et al., 2007). Though the bulk of our calorific needs is supplied by wind pollinated cereals, our major sources for protein, vitamins and micronutrients are derived from crops that are animal pollinated (Chaplin-Kramer et al., 2014). Globally, an estimated 5-8% of crop production would be lost without animal pollination, which would require a significant shift in human diets and undermine the provision of essential micronutrients and vitamins (Potts et al., 2016). More so, animal pollination improves yield quality such as fruit shape, market value and shelf life compared with wind or self-pollination (Klatt et al., 2014). Taken together, the contribution of animal pollination to global crop yield is valued to be \$235-577 billion annually (Potts et al., 2016).

Bees are the most important group of pollinators since they visit more than 90% of the leading 107 crop types (Klein et al., 2007). While the cultivation of pollinator-dependent crops continues to rise, and in concert with that the demand for crop pollination services (Aizen et al., 2009; Aizen and Harder, 2009; Biesmeijer et al., 2006), wild bee abundances and diversity are continuously declining (Biesmeijer et al., 2006; Duchenne et al., 2020b; Zattara and Aizen, 2021). Ensuing these diverging trends, yields of pollinator-dependent crops are more variable than those of pollinator-independent crops, suggesting that inadequate pollination can lead to yield instability (Aizen et al., 2009; Garibaldi et al., 2016, 2011). In fact, inadequate flower visitor density and richness are the most important contributors of yield gaps for 33 different pollinator-dependent crops (Garibaldi et al., 2016). This bleak scenario of a looming ‘pollination crisis’ threatening global food supply (Holden, 2006), calls for more detailed investigations on the dependence of crop yields on pollinators and the current degree of pollination shortage (i.e. yield gaps driven by inadequate pollinator visitations (Garibaldi et al., 2011)) in agricultural landscapes.

Honey bees (*Apis mellifera* L.) are considered the most economically important pollinator species for crop production and their colonies are managed for both honey production and crop pollination (Aizen and Harder, 2009; Klein et al., 2007). Nonetheless, wild bees such as bumble bees (*Bombus* spp.) and solitary bees contribute substantially to crop pollination and many crops are more efficiently pollinated by wild bees

(Eraerts et al., 2020; Nicholson and Ricketts, 2019; Rader et al., 2012). For example, flowers with deep corollas such as clover are more attractive to bumble bees, and alfalfa is primarily visited by alkali bees (*Nomia melanderi* Cockerell) and mining bees (*Andrena* spp.) (Batra, 1976; Bohart, 1957). Furthermore, there is clear evidence that higher pollinator species richness increases pollination service supply to crops, emphasising the need for diverse species communities to ensure sustainable crop pollination (Dainese et al., 2019). It is therefore important to manage agricultural landscapes such that it can support a wide variety of pollinating species.

Biological pest control

Pest infestation contributes significantly to yield instability with an average of 35% of global potential yield being lost due to pre-harvest pests (Oerke, 2006; Popp et al., 2013). Among pests, insects are responsible for an estimated 14% of crop losses (Pimentel, 2009). Increased agricultural pesticide use nearly doubled crop harvests worldwide between 1965 and 1990 (Popp et al., 2013). However, growing concerns surrounding the negative impacts of chemical pesticides on human health, non-target organisms, such as pollinators and natural enemies of pests, the environment, and long-term crop productivity due to developing pesticide resistance have prompted more sustainable management strategies. Integrated pest management (IPM), considers chemical inputs as a last resort and instead relies more on natural control mechanisms (Stern et al., 1959). Biological control by natural enemies of pests has become an important component of pesticide-free insect pest management strategies (Letourneau et al., 2009). Consequently, a pivotal part of biological pest control is to gain a thorough understanding of the ecology of natural enemies such as which habitat types they require to fulfil their lifecycles or how crop management affects their populations, in order to enhance their abundances.

One of the best studied biological pest control systems is that of aphids, which are among the most damaging insect pests worldwide (Zehnder et al., 2007). Aphids are attacked by a range of generalist predators (e.g. spiders and ground beetles), predominantly aphidophagous predators (e.g. ladybird beetles or lacewing larva) and more specialised parasitic wasps (Diehl et al., 2013; Martin et al., 2015). A meta-analysis on predator exclusion experiments demonstrated that aphid populations were significantly suppressed by natural enemies in nearly 80% of the 168 case

studies that were analysed (Diehl et al., 2013). However, the effectiveness of natural enemies to control aphids is affected by landscape complexity, climatic conditions and host plant species (Diehl et al., 2013). For example, natural enemies were more successful in suppressing aphid populations in complex agricultural landscapes than in simple agricultural landscapes (Alignier et al., 2014; Martin et al., 2015), and less successful in reducing aphid populations on legumes, since such nitrogen-rich plants favour fast aphid population growth (Diehl et al., 2013).

Ecosystem services under land use and climate change

Up until recently, ecosystem services such as insect pollination, biological pest control and crop yield have mostly been studied in isolation. Yet, emerging evidence highlights the importance of considering interactions among ecosystem services and with crop management factors (Tamburini et al., 2019), land use (Redhead et al., 2020) or climate change stressors (Bishop et al., 2016). Simultaneous insect pollination and biological pest control, for example, synergistically increase yield (Lundin et al., 2013), proximity to semi-natural habitat (SNH) improves crop yield resilience to environmental perturbations (Redhead et al., 2020), and the benefit of insect pollination to yield was higher in plants subjected to heat-stress (Bishop et al., 2016).

1.2 Ecological intensification

Ecological intensification attempts to sustainably intensify crop production. The concept aims to replace chemical and synthetic inputs, such as pesticides and fertilisers by enhancing beneficial arthropods and their habitats, and so harnessing the ecosystem services they provide (Bommarco et al., 2013). For ecological intensification to be most effective for crop production, we need to identify what type of land use at different scales, crop management and which abiotic and biotic stressors limit population growth of beneficial insect communities and services they provide (Schellhorn et al., 2015). The integration of such knowledge will enable us to compose a toolbox with context-appropriate methods to ecologically intensify crop production and reduce yield gaps (Bommarco et al., 2013; Redhead et al., 2020).

1.2.1 Landscape scale

At a landscape scale, larger areas of natural habitats such as forest patches, grasslands and a complex mosaic of field margins provide beneficial insects with more diverse food resources and nesting and overwintering opportunities, which subsequently can promote species diversity, population size and ecosystem function resilience (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Hass et al., 2018; Hinsley and Bellamy, 2000; Oliver et al., 2015; Thies and Tschardtke, 1999). Natural enemies of pests and pollinators differ in their foraging range (Tschardtke et al., 2005) and species with limited dispersal abilities therefore require habitat connectivity to disperse between similar habitat patches (Bianchi et al., 2006; Carrié et al., 2017; Diekötter et al., 2008). However, given rising demand for agricultural products (Alexandratos and Bruinsma, 2012; Godfray et al., 2010; Tilman et al., 2011), setting aside land from crop production to preserve natural habitats is becoming increasingly challenging to realise (Hodge et al., 2015). More recent research highlights the potential of increasing crop diversity, by enhancing the richness and evenness of crops grown in the landscape, as a way to re-diversify intensive agricultural landscapes without taking land out of crop production (Fahrig et al., 2011). Different crop species can provide a more diverse mosaic of food resources and habitat structures, and thereby support higher populations and species diversity of beneficial insects (Aguilera et al., 2020; Redlich et al., 2018; Sirami et al., 2019).

1.2.2 Local scale

At field scale, farming practices such as reduced tillage (Rusch et al., 2011; Tamburini et al., 2016), diversified crop rotations (O'Rourke et al., 2008; Rusch et al., 2013), planting flower-rich field margins (Blaauw and Isaacs, 2014; Carvalheiro et al., 2012; Tschumi et al., 2015) or allowing weeds to exist (Carvalheiro et al., 2011) enhance natural predator and pollinator abundances and species diversity (Letourneau et al., 2009). The establishment of flower strips or hedgerows are among the most common local diversification strategies applied to foster biodiversity and ecosystem services - not least because they are subsidised by the Common Agricultural Policy (CAP) in the European Union (EU) (Albrecht et al., 2020). By providing more diverse and continuous floral resources, flower strips can enhance habitat connectivity and resource continuity and so

promote natural enemies of pests and pollinators into adjacent crop fields (Blaauw and Isaacs, 2014; Holland et al., 2016; Rundlöf et al., 2018; Tschumi et al., 2016). They can also enhance biological pest control (Blaauw and Isaacs, 2012; Tschumi et al., 2016) and insect pollination (Blaauw and Isaacs, 2014; Sutter et al., 2018) respectively, and in some cases increase crop yield (Pywell et al., 2015; Rundlöf et al., 2018). Nonetheless, their effectiveness as an ecological intensification strategy remains complex and not seldom flower strips attract beneficial insects within the floral planting, but the insects fail to disperse into the adjacent crop (Lowe et al., 2021; Lundin et al., 2017; Nicholson et al., 2020; Sardiñas and Kremen, 2015). In particular, it is poorly understood how flower strips impact mass-flowering crops that provide floral resources themselves but are relying on insect pollination to maximise yield. According to the “exporter” hypothesis (Kremen et al., 2019), flower strips enhance ecosystem services in the adjacent crop via functional spill over. In contrast, according to the “concentrator” hypothesis (Kremen et al., 2019), flower strips temporarily compete with flowering crops by distracting beneficial insects from the fields (Nicholson et al., 2019). Hence, the benefits of flower strips are crop and region specific and more comprehensive assessments are needed to understand in which contexts they can support crop production.

Adding to the complexity of local ecological intensification strategies comes the fact that they are rarely applied in isolation from other management strategies. Yet, little is known about the effectiveness of local diversification strategies when they are integrated alongside conventional intensification strategies. The supplementation of managed honey bee hives to flowering crop fields, for example, is a common practice to boost crop pollination, where pollination by wild pollinators is inadequate (Breeze et al., 2014; Cunningham and Le Feuvre, 2013; Marini et al., 2012). Increased densities of managed honey bees can, however, deter wild bees from crop fields (Artz et al., 2011; Lindström et al., 2016) due to competition for floral resources (Wojcik et al., 2018). It is poorly understood to what degree flower strips can benefit wild pollinators in the presence of managed honey bees (but see Angelella et al., 2021). It is also unclear if increased honey bee densities compete for flower resources with natural enemies of pests and might thereby weaken biological pest control. As such, we need to gain a better understanding of how ecological intensification practices

interact with common conventional practices to shape arthropod communities and ecosystem services.

2. Aims

In my thesis I aimed to identify how diversification of agroecosystems at different scales influences arthropod communities and ecosystem services, and how these services bolster crop production despite climate change stressors.

Specifically, my objectives were to:

- Explore how diversification strategies at landscape scale (crop diversity and proportion of semi-natural habitat), and local field scale (flower strips) influence pollinator communities in crop fields and the wider landscape (papers I - III), and how added honey bee hives influence the effects of flower strips (paper II and III)
- Assess how flower strips and honey bee hive supplementation, separately and combined, influence natural enemy and pest communities, and biological pest control in crop fields (paper II)
- Estimate the contribution of insect pollination on yield components and how the insect pollination benefit is modified by land use and climate change stressors (papers I, II and IV)
- Investigate the effects of land use change and climate change stressors on crop yield (papers I, II and IV)

Faba bean crop production served as a model system to tackle these aims.

3. Methods

3.1 Study system

3.1.1 Faba bean cultivation

Faba bean (*Vicia faba* L.) is among the oldest crops grown. Archeological findings suggest that they were already domesticated in the Southern Levant during the period when farming first appeared (Caracuta et al., 2015). Today, faba bean is one of the most important legume crops worldwide (Karkanis et al., 2018). Faba bean is rich in protein and grown mostly for fodder in Europe but constitutes an important staple food in countries like China, Ethiopia, and the Mediterranean region (Jensen et al., 2010). The cultivation of faba bean offers some key environmental benefits for sustainable agriculture. Faba bean improves soil fertility and its high efficiency in symbiotically fixing atmospheric nitrogen reduces the need for fertilisers for subsequent crops (Karkanis et al., 2018). As a result, integrating faba bean in the crop rotation enables the reduction of both fossil fuel consumption and greenhouse gas emissions associated with the production and use of synthetic fertilisers (Jensen et al., 2010; Köpke and Nemecek, 2010). Furthermore, faba bean cultivation enhances bumble bee densities in the wider landscape by providing late-season floral resources (Beyer et al., 2020).

Despite the many benefits of faba bean cultivation, the global acreage of faba bean has steadily declined over the past half century not least due to yield instabilities associated to abiotic and biotic stressors (Karkanis et al., 2018). In addition, the invention of the Haber-Bosch method to produce

artificial fertilisers lessened the importance of legumes as natural nitrogen fixators (Jensen et al., 2010; Karkanis et al., 2018). In contrast to the more long-term decrease, however, faba bean acreage has generally increased in Sweden and elsewhere in Europe over the past ten years (Fig. 1) (Swedish Board of Agriculture, 2020a). The increase in cropping area of faba bean in Europe is a response to the need for substituting the disputed import of soy bean with locally produced plant-based protein crops and is encouraged by EU subsidies under the reformed CAP for more diversified crop rotations (Zander et al., 2016).

Faba bean cropping area (ha) in Sweden between 2006-2020

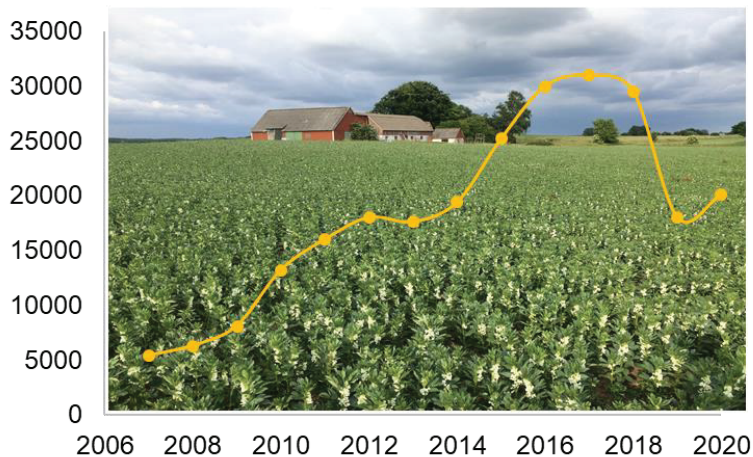


Figure 1. Faba bean cropping area (hectares) in Sweden statically increased between 2006 and 2018. Due to a shortage and bad quality of seeds following the 2018 heatwave and drought (Swedish Board of Agriculture, 2020a), faba bean cropping area dropped in 2019 and 2020. Photo: Chloë Raderschall

3.1.2 Faba bean pollination

Faba bean flowers are partially dependent on cross-pollination by insects. Though there is a general understanding that faba bean yield benefits from insect pollination, the insect pollination dependence reported varies greatly, which is mostly due to cultivar differences (Bishop and Nakagawa, *in press*). On average, however, faba bean yield is 32.9% lower in plants that were not insect pollinated compared to insect pollinated plants (Bishop and Nakagawa, *in press*).

A faba bean plant can produce 50-80 flowers, yet a large proportion is shed during the growing season (Free, 1993) partly as a result of inadequate cross-pollination (Suso et al., 1996). The flowers produce high quality pollen (Pamminger et al., 2019), yet only small amounts of nectar at the bottom of the corolla. Faba bean nectar is challenging to access by short-tongued pollinators through legitimate visits, thus many short-tongued species such as buff-tailed bumble bees (*Bombus terrestris* L.) and honey bees instead rob nectar by biting a hole at the base of the corolla (Tasei, 1976). In addition to the flowers, extra floral nectaries (EFN) secrete beads of nectar on stipules, which are located below the flowers, and attract pollinators and natural enemies of pests to the crop when flowers are unavailable (Stoddard and Bond, 1987). In Europe, the dominant flower visitors of faba bean are honey bees and bumble bees, while solitary bees are only occasionally observed (Marzinzig et al., 2018).

3.1.3 Faba bean arthropod pest susceptibility and control

Faba bean plants are attractive to over 70 species of arthropod pests worldwide (Stoddard et al., 2010). Among these, aphids are considered the most serious and damaging insect pest worldwide (Stoddard et al., 2010). Aphids cause direct faba bean yield losses by feeding on the plant phloem, which impacts the plant's photosynthetic ability, and indirect damage by vectoring a range of diseases (Cammell and Way, 1983). In northern Europe, black bean aphids (*Aphis fabae* Scopoli) can cause yield losses of up to 50% (Hansen et al., 2008). Occasionally, also other aphid species such as pea aphids (*Acyrtosiphon pisum* Harris) and vetch aphids (*Megoura viciae* Buckton) attack faba bean plants (Sanders et al., 2018).

Another economically significant insect pest in Europe is the broad bean beetle (*Bruchus rufimanus* Boheman). Unlike aphids, broad bean beetles do not affect yield by impacting the crop's physiology. Instead, this pest, whose larva develop inside the beans, significantly reduces the quantity and quality of faba bean products and its proceeds (Segers et al., 2021). Beans infested with broad bean beetles are lower in weight due to the endosperm consumption of the developing larvae, and beans with adult beetle emergence holes are more susceptible to fungal diseases, less likely to germinate (Khelfane-Goucem and Medjdoub-Bensaad, 2016) and of reduced value to the food and feed market, which have strict quality

standards that allow a maximum of 3% and 10% of infested beans, respectively (Segers et al., 2021).

Chemical control options for faba bean pests in Sweden are limited. The only insecticide registered for use against broad bean beetles in Sweden was Biscaya but its registration ended in 2020 (Swedish Board of Agriculture, 2020b) and its efficacy was limited because only few treatments per season were permitted and the dense canopy of faba bean prevents proper penetration to the pods, on which the eggs are laid (Segers et al., 2021). Alternative control measures against broad bean beetles include semiochemical trapping (Bruce et al., 2011), the selection of more resistant varieties (Seidenglanz and Huňady, 2016), or early harvesting to intervene with the beetle's life cycle (Bachmann et al., 2020). Faba bean pests are also attacked by a range of natural predators. Ladybird beetle adults and larva, hoverfly larva and lacewing larva predate on aphids. In addition, aphids are parasitised by specialised parasitoids (Sanders et al., 2018). The parasitic wasp *Triaspis thoracicus* Curtis is known to parasitise developing broad bean beetles eggs (Seidenglanz and Huňady, 2016), but its potential as a biological control agent in faba bean production remains to be evaluated.

3.2 Experimental design

For my thesis work I conducted two large-scale landscape studies with commercially managed faba bean fields (papers I-III), and one field plot experiment with cages (paper IV). In 2017, I did an observational field study in faba bean fields surrounded by landscapes with independent gradients in crop diversity and proportion SNH (paper I). In 2018, I experimentally manipulated local flower resource availability by sowing annual flower strips, and resource competition by supplementing managed honey bee hives in a crossed design (papers II and III). In 2019, I conducted a cage experiment, where I manipulated the levels of insect pollination, water stress and insect herbivory (paper IV).

3.2.1 Field surveys

Field surveys, where I worked with commercially grown faba bean fields (papers I, II, III) were located in Skåne, the southernmost province of

Sweden. Skåne spans across approximately 100 by 100 km of which approximately 40% is arable land (Statistics Sweden, 2018). The most common crops cultivated in this province are (in descending order) winter wheat, leys, spring barley and winter oilseed rape, but numerous other crops, including faba bean, are also grown (Statistics Sweden, 2018). Faba bean growers were located with the help of seed companies and existing relations and contacted in spring for permission to work in their fields.

Landscape level diversification: crop diversity and proportion of SNH (paper I)

To investigate landscape effects of diversification on arthropod communities and ecosystem services, I selected 14 conventionally managed faba bean fields in 2017 along uncorrelated gradients of crop diversity and SNH. Circular landscape buffers surrounding the focal faba bean fields were characterised within a 1.5 km radius from field centres for the proportion of SNH and crop diversity using a GIS layer that contains pasture and crop information for each farm in each year. Crop and pasture information were obtained from the Integrated Administration and Control System (IACS), administered by the Swedish Board of Agriculture. In addition, I used a digitalised Swedish topographic map (Terrängkartan, Lantmäteriet, 2018) in ArcMap software (ESRI, 2015) to map other land use types such as forest patches.

To calculate crop diversity, I categorised all crops that were grown within the circular landscapes surrounding focal faba bean fields into 14 crop categories: beets, spring sown brassicas, winter sown brassicas, spring sown cereals, winter sown cereals, clovers, corn, fallow, leys, potato, pulses, trees, vegetables/fruits/berries and other. After obtaining the cover area of each crop category in each landscape buffer, I calculated the Shannon-Wiener index (hereafter Shannon index) using the “vegan” package in R (Oksanen et al., 2019) that would reflect the level of crop diversity in each experimental landscape. In addition, the proportion of SNH in each landscape was calculated as the percentage cover of pastures and forest patches within each circular landscape. The crop diversity in the landscapes surrounding the focal faba bean fields ranged from 1.3-1.9 in Shannon index (Fig. 2), and the proportion of SNH from 0 – 0.15.

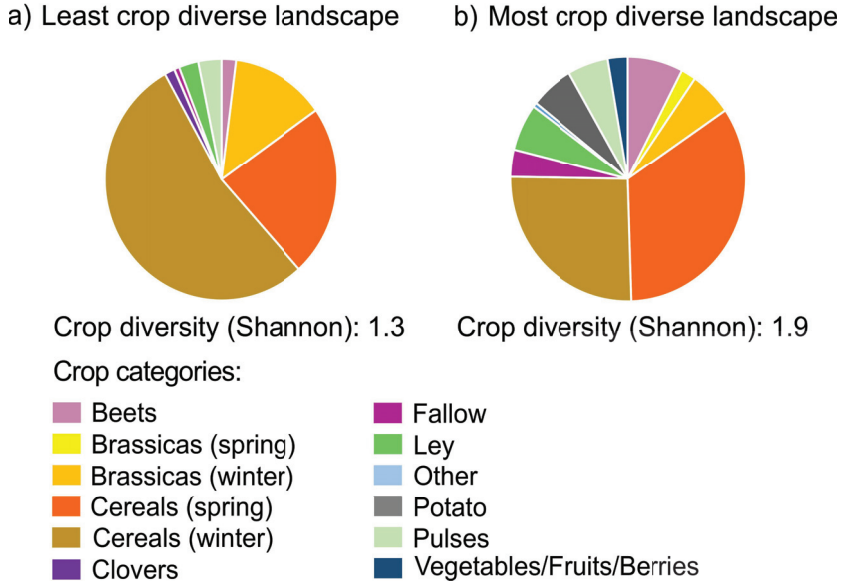


Figure 2. Proportional crop category contributions to the a) least crop diverse and b) most crop diverse landscapes.

Local diversification: flower strips and honey bee hives (paper II and III)

To investigate local effects of diversification on arthropod communities and ecosystem services, I selected 17 organic faba bean fields and assigned them to one of four treatments. To augment the local availability and continuity of floral resources, I sowed flower strips to nine faba bean fields while in the remaining eight fields a 5 m wide strip of faba bean served as a control strip. To additionally manipulate resource competition, I collaborated with local beekeepers and added the equivalent of ten full-strength honey bee (*Apis mellifera* L.) hives to four of the faba bean fields of each flower strip treatment, while nine fields were assigned as controls without honey bee hives (Fig. 3).

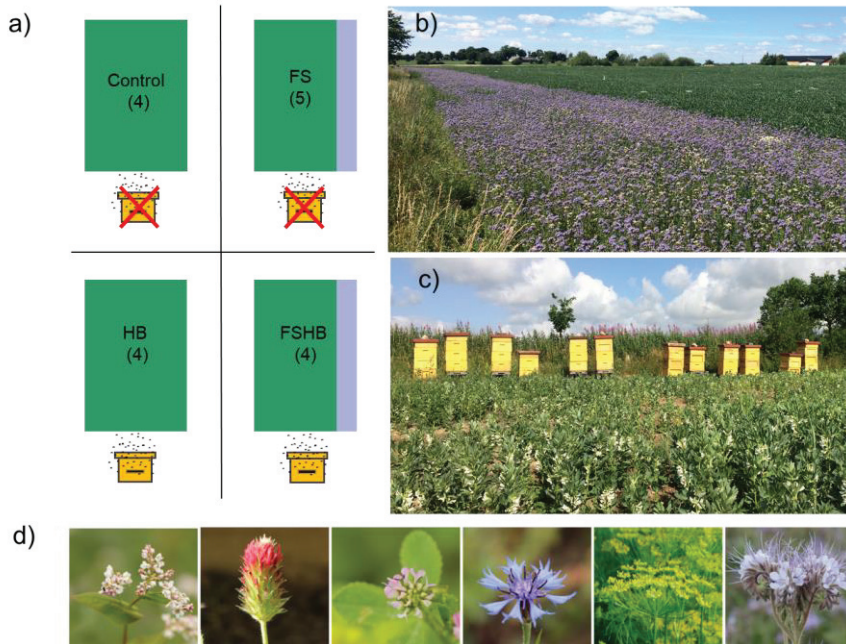


Figure 3. a) Schematic of the four treatments and the respective number of replications within parenthesis. Top left to bottom right: faba bean control field; faba bean field with sown flower strip and without honey bee hives (FS); faba bean field without a flower strip and with honey bee hives (HB) and faba bean field with added honey bee hives and with flower strip (FSHB). b) Photo of a faba bean field with a sown flower strip. c) Photo of a faba bean field supplemented with honey bee hives. d) Sown flower species from left to right: buckwheat, crimson clover, Persian clover, cornflower, dill and phacelia. Photos: Chloë Raderschall and Elisabeth Ögren (dill).

I sowed flower strips along the edge of nine faba bean fields in spring 2018. The composition of the flower strip species was chosen to attract both wild pollinators and natural enemies of faba bean pests. Furthermore, the flower species were chosen to vary in floral morphology and flowering phenology such that the flower strip would provide continuous floral and EFN resources throughout the flowering period of faba bean and beyond until late summer. The following six plant species were selected: buckwheat (*Fagopyrum esculentum* Moench, Polygonacea), crimson clover (*Trifolium incarnatum* L., Fabaceae), Persian clover (*Trifolium resupinatum* L., Fabaceae), cornflower (*Centaurea cyanus* L., Asteraceae), dill (*Anethum graveolens* L., Apiaceae) and phacelia (*Phacelia tanacetifolia* Benth, Boraginaceae).

In Sweden, beekeepers are required to report the location of their beehives to the County Administrative Board. Using this hive location information, I mapped all honey bee hives within a 2 km radius from our focal faba bean fields to reduce stationary honey bee hives in the honey bee control landscapes by asking beekeepers to remove hives away from focal fields. The landscape composition surrounding each faba bean field was characterised within 2 km radii from field centres. Faba bean fields were selected and assigned to treatments such that the proportions of SNH, including forest and pasture, and winter oilseed rape (*Brassica napus* L.) and turnip rape (*Brassica rapa* L.) were balanced among treatments. Pasture and crop data were extracted from a GIS layer obtained from the Integrated Administration and Control System (IACS) and forest cover from a digitalised topographic map (Terrängkartan, Lantmäteriet, 2018) in ArcMap software.

3.2.2 Cage experiment

During the first two field seasons, I assessed how insect pollination and pest pressure affect yield in commercial faba bean fields. However, faba bean yields in Skåne during those two growing seasons were primarily limited by extreme weather events (Fig. 4). In 2017, our experimental fields were subjected to unusually cold and wet weather, which according to farmer questionnaires, was the factor limiting yields the most. Conversely, 2018 was an exceptionally hot and dry growing season in central and northern Europe (Toreti et al., 2019; Wilcke et al., 2020), and many faba bean fields suffered from water stress. As a consequence, faba bean yield across Sweden was on average 64% lower than the five year average (Swedish Board of Agriculture, 2018).



Figure 4. Impressions from two experimental fields impacted by extreme weather events. Left: A water-logged faba bean field at harvest in 2017; right: a faba bean field at harvest in 2018 impacted by drought and heat stress. Photos: Carol Högfeltdt (2017) and Hanna Olsson (2018).

Having observed the importance of water availability for yield in my experimental fields sparked the idea to design a study, where I could experimentally manipulate the levels of water availability, insect pollination and insect herbivory to investigate how they interactively shape faba bean yield (paper IV). To do this, I set up a field experiment in a faba bean field near Uppsala, Sweden in 2019. I erected 24 cages (2 x 2 x 2 meters), that I placed under rainout shelters to exclude natural precipitation (Fig. 5a). In a randomised complete block design replicated in six blocks, I crossed the water availability treatment (well-watered *versus* increasingly water-stressed; see below) with the pollination treatment (insect pollination *versus* self-pollination, Fig. 5b). Nested within the block design, I set up a split-plot design for the insect herbivory treatment, in which each cage contained two subplots assigned to one of two insect herbivory treatments i.e. 24 aphid-free and 24 aphid-infested subplots (Fig. 5b).

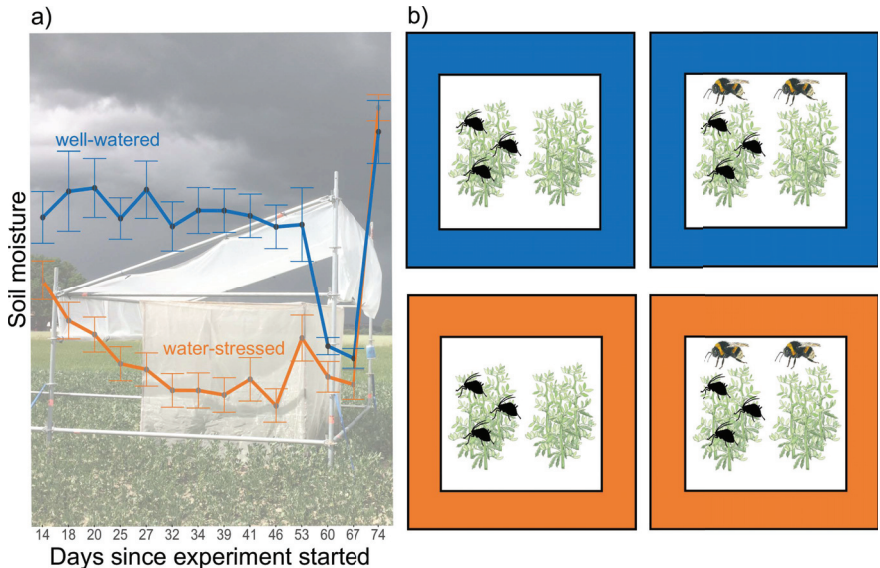


Figure 5. a) a rainout shelter with a cage underneath overlaid by average soil moisture readings of well-watered and water-stressed plots over the experimental period; b) schematic of the four treatments with well-watered (blue) and water-stressed (orange) plots containing faba bean plants that are either pollinated by bumble bees or self-pollinated, and either under herbivory attack from aphids or free from herbivory. Figure adapted from Raderschall et al. (2021).

To induce increasing levels of water stress, I excluded natural precipitation for 46 days. Conversely, the well-watered treatment was regularly irrigated to keep soil moisture levels nearly stable. Each plot was irrigated approximately the amount the plants lost through evapotranspiration during the previous week, which was estimated using FAO CROPWAT 8.0, which uses the Penman-Monteith formula (Allen et al., 1998). In the end, the total monthly water inputs were in line with precipitation averages in the region.

For the insect herbivory treatment, I inoculated ten plants within each cage with small colonies of black bean aphid, whose infestations levels were then continuously recorded by assigning one infestation class to each plant: 0: 0 aphids, 1: 1-5, 2: 6-25, 3: 26-125, 4: 126-625 and 5: >625 aphids (Grechi et al., 2008).

To establish two levels of insect pollination, I supplemented half the cages with one hive of buff-tailed bumble bees (*Bombus terrestris* L.) containing approximately 10 workers (Natupol Seeds, Koppert Biological Systems, the Netherlands).

3.3 Sampling methodologies

3.3.1 Pollinator visitation and foraging behaviour

To estimate pollinator densities and predominant foraging behaviours in commercial faba bean fields (papers I and II), I did transect counts of all flower and EFN visiting insects (hereafter pollinators). Along with each visitation count, I also noted whether the individual 1) legitimately visited a faba bean flower, 2) robbed nectar or 3) visited an EFN (Fig. 6). In paper IV, where buff-tailed bumble bees were foraging within cages, I recorded all bumble bees visiting faba bean flowers or EFN and their foraging behaviour on 10 randomly marked plants over 10 mins. At the end of each sampling session, I estimated the floral resources provided by faba bean (papers I, II and IV), flower strips and landscape transects (papers II and III).



Figure 6. Sampling pollinators along transects (top left) and inside cages (top right). The three pollinator behaviours that can be observed on faba bean plants. Bottom left to right: A buff-tailed bumble bee (*Bombus terrestris* L.) legitimately visiting a faba bean flower; robbing nectar via a bitten hole in base of the corolla; and foraging nectar secreted from an EFN. Photos: Jenny Jewert (top right) and Chloë Raderschall (others).

3.3.2 Vegetation-dwelling arthropods

To identify the arthropod community dwelling on faba bean plants (paper II), I screened randomly selected plants along transects from bottom to top for the common faba bean insect pests such as black bean aphids, pea aphids and broad bean beetles and their natural enemies including ladybird beetles (Coccinellidae), lacewing (Chrysopidae) and hoverfly (Syrphidae) larva (Fig. 7). To estimate pea aphid parasitisation rate, I counted parasitised aphid mummies.



Figure 7. Natural enemies of aphids. Left to right: a seven-spotted ladybird beetle (*Coccinella septempunctata* L.) feeding on black bean aphids (*Aphis fabae* Scopoli); a hoverfly (Syrphidae) larva feeding on black bean aphids and a lacewing larva (Chrysopidae) looking for prey. Photos: Chloë Raderschall

3.3.3 Ground-dwelling predators

To identify the ground-dwelling predator community (paper II), I placed wet pitfall traps along transects in the faba bean field and in the flower strip. Pitfall traps were emptied and refilled weekly and their contents stored in 70% ethanol. In the laboratory, all collected carabid beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Araneae) were morphologically identified to species or genus level.

3.3.4 Broad bean beetle infestation and parasitism

To estimate broad bean beetle infestation of beans and the parasitism rate of the beetles (paper II), I collected mature pods at harvest and transferred them into cardboard tubes to rear both the broad bean beetles and their parasitoids. After a few months, all pods were opened and all beans counted and inspected for broad bean beetle and parasitoid emergence holes. The emergence holes between the beetles and the parasitoids can be differentiated due to their size difference (Fig. 8). This allowed us to estimate the broad bean beetle infestation rate per bean and the parasitism rate per broad bean beetle. A subsample of parasitoids was determined to species level by a taxonomist to confirm that they are *Triaspis thoracicus* Curtis (Braconidae). This wasp species is known to parasitise broad bean beetles (Seidenglanz and Huňady, 2016) and exists in Sweden, but until now there were no records on their potential to parasitise broad bean beetles in Sweden.



Figure 8. A faba bean with a broad bean beetle (*Bruchus rufimanus* Boheman) (left) and parasitoid wasp (*Triaspis thoracicus* Curtis) (right) emerging. Photos: Chloë Raderschall

3.3.5 Insect pollination benefit

I estimated the benefit of insect pollination for faba bean yield components by selecting plant pairs along transects, where one plant was bagged to exclude insect pollination while the other plant was open and accessible for pollinators (papers I and II). In paper IV, I used cages either with or without bumble bee hives inside such that plants inside cages without hives were not insect pollinated. At pod maturity, all pods of experimental plants were harvested. I counted the number of pods containing beans per plant. Pods that did not contain any beans, were excluded from further analysis. I counted the beans per pod and dried all beans at 65°C for 48 hours. Dry bean mass was weighed for each plant. Individual bean weight was calculated by dividing bean mass with the total number of beans per plant.

3.3.6 Yield

Faba bean yield was measured on all our experimental fields (papers I, II and IV). Several 0.36 m² quadrats were placed along transects or inside cages and all faba bean plants manually harvested. Harvesting samples were dried at 65°C for 48 hours. Beans per quadrat were counted and weighed, while the pod husks, leaves and stems were weighed to obtain the above ground biomass.

4. Results and discussion

In my thesis, I present evidence that both landscape level and local field diversification strategies affected arthropod communities in agricultural fields, the surrounding landscape and the ecosystem services they provide (Fig. 9). Landscape crop diversity and higher proportion of SNH enhanced bumble bee densities in flowering faba bean fields (paper I). Flower strips sown along field margins enhanced ground spiders in faba bean fields (paper II), and enhanced bumble bee queen abundances in landscapes with few honey bee hives (paper III). Honey bee hive supplementation did not increase crop yield but enhanced the overall densities of ladybird beetles and black bean aphids along the field edge (paper II). Insect pollinated plants produced more bean mass per plant compared with bagged plants that were excluded from pollinator visits (papers I, II and IV). The insect pollination benefit reduced with increasing SNH cover in the landscape (paper I) but was independent from water stress and herbivory (paper IV). Crop yield was higher in landscapes with more SNH cover (paper I), and yield was maximised when abiotic and biotic stressors are reduced simultaneously (paper IV), which is particularly relevant to consider given climate change (Fig. 10).

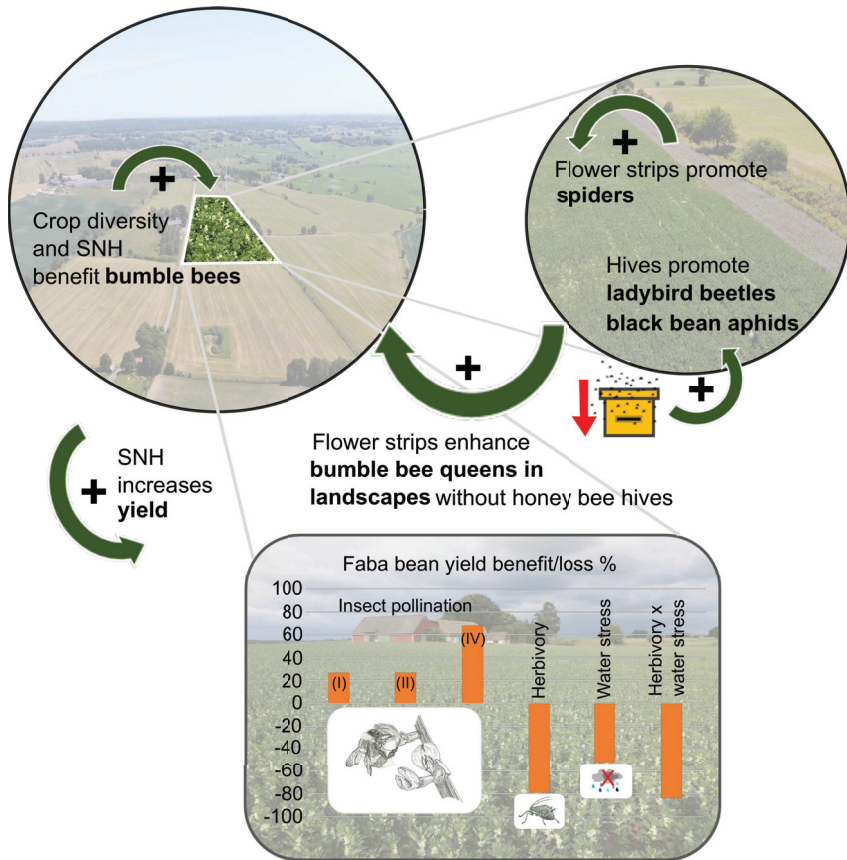


Figure 9. Summary of key results presented in this thesis. Higher landscape crop diversity and proportion of semi-natural habitat (SNH) promoted bumble bees in faba bean fields. SNH also increased faba bean yield, but the effect was not driven by pollinators. Flower strips facilitated ground predators such as spiders. Flower strips also enhanced bumble bee queen abundances in landscapes without honey bee hives. Honey bee hives promoted overall ladybird beetle densities and black bean aphids along the field edge. Faba bean yield benefited from insect pollination. Bean mass per plants was 27% higher in open pollinated compared to bagged plants (papers I and II), and yield (kg per hectare) was 68% higher in cages with bumble bees compared to cages without bumble bees, and the effect was independent of aphid herbivory and water stress (paper IV). On their own, insect herbivory and water stress reduced yield by 79% and 52%, respectively. However, the combined effect of insect herbivory and water stress reduced yield by 84%. Photos and illustrations: Oskar Rennstam Rubbmark (aerial photographs) and Chloë Raderschall (others).

4.1 Diversification strategies to promote pollinators

4.1.1 Landscape level diversification

At a landscape scale, both higher crop diversity and proportion of SNH enhanced bumble bee visitations to faba bean flowers and EFN (paper I). I conclude that a more diverse composition of crops in the landscape creates more varied and continuous food resources (Fahrig et al., 2011; Schellhorn et al., 2015; Vasseur et al., 2013), while SNH provide pivotal foraging and nesting resources (Boetzi et al., 2021; Öckinger and Smith, 2007). The positive effect of remaining patches of SNH, for wild and managed pollinators in agricultural landscapes have been described before (Kennedy et al., 2013; Nayak et al., 2015; Rivers-Moore et al., 2020). My thesis contributes to existing research by highlighting that enhanced landscape crop diversity can complement SNH in the landscape rather than replacing it. The positive effect of crop diversity on bumble bee densities that I found contrasts earlier observations, where wild bee densities decreased with (Hass et al., 2018) or were unaffected by (Fahrig et al., 2015) crop diversity. I propose that the identity of crops that become more or less abundant with increasing landscape crop diversity are pivotal for the outcome crop diversity has on pollinators.

4.1.2 Local diversification

Sown annual flower strips affected the distribution of wild pollinator densities and the foraging behaviour of bumble bees within faba bean fields. In fields with flower strips, bumble bee densities were lower along the field edge than in the field interior, while there was no difference in bumble bee densities with distance from field edge in fields without flower strips (paper II). I suggest that bumble bees reduced in line with the “concentrator hypothesis”, where bumble bees are more attracted to flowers in the strip (e.g. phacelia) than to the crop flowers. Thus, flower strips and crop flowers temporarily competed for bumble bee visits (Albrecht et al., 2020; Kremen et al., 2019). Silver Y moth densities tended to be higher along the field edge in fields with flower strips compared to fields without flower strips, suggesting that flower strips facilitated moths into the crop (paper II). The densities of silver Y moths also decreased towards the field interior in fields with a flower strip. The proportion of legitimately visiting bumble bees was also higher closer to the flower strip compared to field

interiors and did not differ in fields without flower strips (paper II). I suggest that phacelia flowers in the strip primarily attracted nectar visiting bumble bees, while pollen foragers continued to forage on faba bean, whose pollen is particularly rich in protein (Hanley et al., 2008; Pamminger et al., 2019). As a result, flower strips selected for legitimately visiting bumble bees. Even though flower strips influenced pollinators locally, I found no overall positive effect of flower strips on pollinator densities in the faba bean fields. It is possible that the relatively small areas of flower strips (range: 0.1-0.5 ha) within the simplified agricultural landscape did not provide sufficient floral resources to recruit bees from the surrounding landscape. Alternatively, the flower strip blooming period might have occurred too late in respect to the faba bean bloom to attract more pollinators from the wider landscape to the faba bean fields. A late frost delayed sowing of the flower strip and consequently its blooming period, while the succeeding hot and dry summer preceded and shortened the faba bean bloom. Together, these unusual weather events lead to a very brief blooming overlap between the two habitats.

Flower strips did, however, enhance bumble bee abundances in the landscape (paper III). I found a tendency for higher bumble bee abundances along flower-rich field borders in landscapes with flower strips and without honey bee hives. Annual flower strips also enhanced the number of bumble bee queens the following spring but only in landscapes with no honey bee hives. The late season floral resources provided by the flower strips might have supported bumble bee queen production in 2018, which occurs in late summer, when floral resources in simplified agricultural landscapes are scarce because most crops stopped flowering (Timberlake et al., 2019). Alternatively, the late season nectar resources provided by the flower strips (Costa et al., 2020) might have boosted bumble bee body size (Grab et al., 2019), which is a critical prerequisite for overwintering survival in queens (Beekman et al., 1998; Costa et al., 2020).

4.2 Effects of flower strips and honey bee hives on natural enemies, pests and biological pest control

Flower strips enhanced overall densities of ground-dwelling spiders and tended to enhance carabid beetle species diversity along the field edge in adjacent faba bean fields (paper II). Flower strips most likely benefit

ground-dwelling predators by providing more complex vegetation structure for shelter and a different microclimate rather than providing food resources (Ditner et al., 2013). Such structural and microclimatic shelters establish soon after sowing, which gave spider populations, in particular, time to establish and disperse into the adjacent crop. Nonetheless, I found no evidence that flower strips reduced the densities of insect pests in faba bean fields. This is in contrast to a recent synthesis, which demonstrated that flower strips enhance pest control on average by 16% in adjacent fields compared to fields without flower strips (Albrecht et al., 2020). It is possible that the relatively late flowering of the flower strip might have prevented sufficiently large colonisation of natural enemies of pests to detect a reduction in aphid densities. Among foliage-dwelling natural enemies, flower strips only tended to enhance ladybird beetles, and only in the field interior. It is likely that some of the ladybird beetles that were recruited remained inside the flower strip rather than dispersed into the crop, which weakened the positive effect of flower strips along the field edge. To confirm this suspicion, it would have been necessary to sample ladybird beetles also in the flower strip.

Adding honey bee hives to flowering faba bean promoted overall ladybird beetle densities and black bean aphid densities along the field edge (paper II). This evidence that honey bee hives can promote natural enemies of pests is novel and deserves more attention in order to understand the underlying mechanism. Future experiments could, for example, measure EFN secretion in faba bean plants both with and without honey bee hive supplementation and test if they differ. Differences in nectar availability might affect ladybird beetle densities and subsequently aphid infestation.

I found a tendency for higher broad bean beetle infestation in fields with honey bee hives and flower strips compared to fields with honey bee hives but that lacked flower strips. In order to better explain the mechanisms driving the interactive effect of honey bee hives and flower strips on broad bean beetle infestation, investigations are needed that monitor the number of broad bean beetles inside flower strips, or explore interactions among pollinators and broad bean beetles. I found that broad bean beetle parasitisation rate was lower in fields with flower strips compared with fields without flower strips, but only along the field edge. It would be interesting to explore if flower strips attract broad bean beetle parasitoids away from faba bean fields and so weaken the parasitisation potential. Alternatively,

flower strips might interfere with the ability of parasitoids to localise broad bean beetle eggs and larvae by masking potential olfactory cues.

4.3 The importance of insect pollination for crop yield

Insect pollination increased faba bean yield components, with bean mass being substantially higher in open pollinated plants compared to bagged plants (papers I, II and IV). In paper I, I show that the insect pollination benefit decreased with increasing SNH cover (Fig. 10a). Thus, while insect pollination was important to close the yield gap associated with low proportions of SNH in the landscape, insect pollination did not affect yield at high proportions of SNH in the landscape. This decrease in insect pollination benefit could be due to faba bean plants being able to compensate more for insufficient insect pollination when they are growing in otherwise favourable conditions in landscapes with more SNH due to e.g. better soil conditions for faba bean (Tamburini et al., 2019). In paper II, I confirmed that insect pollination increases yield components on average by 27%, but the insect pollination benefit was independent of the flower strip and the honey bee hive treatments. Thus, even though supplementing fields with honey bee hives significantly increased the density of honey bees visiting faba bean flowers, and flower strips positively influenced legitimately visiting bumble bees and silver Y moths, neither treatment affected the insect pollination benefit. I therefore conclude that faba bean fields were not pollination limited. In paper IV, the insect pollination benefit was even more pronounced, with faba bean yield from cages with bumble bees being 68% higher than from cages without bumble bees. While the insect pollination benefit for area-based yield was independent of water stress and herbivory by aphids (Fig. 10d, e), the gain in bean mass on individual plants that were both visited by insects and free from aphids was higher than the sum of the bean mass gain in plants that were either visited by insects or free from aphids. Similar synergistic interactions between insect pollination and insect herbivory have been observed in several other crops (Tamburini et al., 2019) and are often explained by reduced pollinator visitations to herbivore-infested plants (Jacobsen and Raguso, 2018). Alternatively, aphid-free plants might have had more resources available to invest, such that more fertilised ovules, as a consequence of insect pollination, developed into mature beans (Lee, 1988).

4.4 Ecological intensification under land use and climate change

Crop yield was higher in landscapes with more SNH (paper I, Fig.10b). Increased pollinator densities were not the driver of high yields associated with higher proportions of SNH because the observed yield increase was unrelated to pollinator densities and driven by bagged plants that were excluded from pollinator visits (Fig. 10a). Instead, the yield increase must have been due to other factors that I could neither control for nor measure such as variation in soil properties associated with the SNH gradient (Bartomeus et al., 2015). From an agricultural perspective, retaining SNH patches in agricultural landscapes benefits both crop production and wild pollinator densities. Faba bean plants in fields with flower strips showed a tendency for higher bean mass per plant (paper II). However, since this effect was independent of whether plants were bagged or open-pollinated, I conclude that the bean mass increase was not driven by pollinators. Instead, I think that this trend was driven by two fields containing flower strips, which were irrigated due to the extreme drought in 2018, and as a result these plants suffered less from water stress and produced higher bean mass.

In the following field season in 2019, I experimentally confirmed that water stress significantly limited yield components in faba bean. I found that gradually increasing water stress culminating around crop flowering and simultaneous aphid herbivory interactively shaped faba bean yield (paper IV, Fig. 10c). Aphid herbivory alone reduced yield by 79%, while water stress reduced yield by 52%. When the two stressors acted in combination, however, yield loss was less severe (84%) than the sum of the individual stressor effects. However, considering that yield would have been below zero if the two stressors had additive effects (no interaction), and therefore unrealistic, I argue that the combined effect of the stressors was limited by the lower boundary of zero (no yield), and that each stressors caused constant proportional rather than absolute yield losses (Côté et al., 2016). Our results suggest that severe crop yield losses can be avoided when both water stress and insect herbivory are reduced simultaneously. In contrast, reducing only water stress had negligible benefits on yield as long as the crop was impacted by aphid herbivory. Considering that under climate change, extreme weather events inducing water stress in crops are expected to become more frequent (Seneviratne et

al., 2012), it is essential to find sustainable management strategies that minimise the risks of concurrent pest infestations.

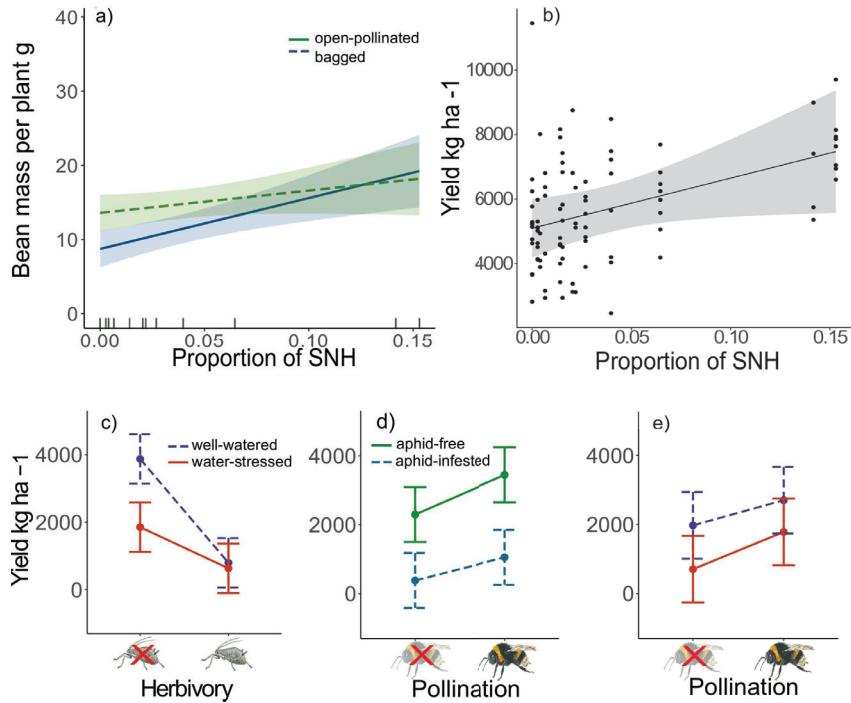


Figure 10. a) Bean mass per plant in open-pollinated (green dashed) and bagged (blue, continuous) plants with increasing proportion of semi-natural habitat (SNH) in the landscape. b-e) Yield per hectare in relation to b) the proportion of SNH in the landscape, c) water and herbivory levels, d) herbivory and pollination levels, and e) water and pollination levels. c-e) well-watered (blue, dashed), water-stressed (orange, continuous), aphid-free (green, continuous, crossed-out aphid symbol), aphid-infested (turquoise, dashed, aphid symbol). Insect pollination (bumble bee symbol), self-pollination (crossed-out bumble bee symbol). Whiskers represent 95% confidence intervals.

5. Conclusions and recommendations

Future food demands should be met by a set of societal adaptations including the reduction of food waste along the food chain, diet shifts away from resource-intensive food, such as meat and dairy products, and more efficient governance of food systems, but crop production also needs to increase (Godfray and Garnett, 2014). As an agroecologist, my aim with this thesis was to contribute to a better understanding on how we can manage and design agroecosystems in a way that crop production can increase sustainably without threatening the environment and its ecosystem functions. The recent integration of empirical research into theoretical principles and frameworks provides a good foundation for the development of informed agroecosystem management that allows for achieving this goal (Landis, 2017). In my thesis, I focused on assessing the effectiveness of diversification strategies at different spatial scales (i.e. landscape crop diversity, the retention of semi-natural habitat (SNH) and the provisioning of annual flower strips) in promoting beneficial arthropods, insect pollination and biological pest control, and enhancing crop yield.

My thesis work showed that at landscape scale increased crop diversity increased bumble bee abundances in crop fields but it did not enhance crop yield (paper I). In contrast, higher proportions of SNH increased both bumble bees and crop yield, albeit the higher bumble bee abundance was not driving the yield increase (paper I). Based on these results, I recommend that future agri-environmental schemes incentivise farmers to lengthen and add crop species to crop rotations to support landscape crop diversity, while the conservation of remaining SNH patches should be maintained. However, not all crops are beneficial for pollinators (Hass et al., 2019). **Therefore, future research should assess the role of functional crop diversity, by distinguishing crop types based on their**

functional importance for pollinators in providing resources rather than merely based on their identity (Fahrig et al., 2011) to see if such an approach can strengthen pollinators even more and lead to enhanced crop yield. Furthermore, it would be interesting to assess the effect of landscape crop diversity over multiple years to test if it can boost bumble bee population growth.

At field scale, annual flower strips failed to recruit more bumble bees to crop fields but I documented behavioural changes and redistributions between crop and flower strip in bumble bees (paper II). Flower strips tended to enhance bumble bees in the wider landscape in late summer, and enhanced bumble bee queen abundances in the following spring, both provided that honey bee densities in the landscape were low (paper III). I propose that both the failure of flower strips to recruit bumble bees into faba bean fields, and the significant positive effect of flower strips on bumble bee queen abundances in the landscape the following spring were in part driven by the unusually hot and dry summer in 2018. Due to the extreme weather, the flower strip and faba bean blooming period barely overlapped, and so the additional floral resources provided by the flower strip might have not been sufficient to attract more bumble bees from the wider landscape into the faba bean field. In contrast, the late-season floral resources provided by the flower strip were particularly essential for bumble bee population growth because the hot and dry weather hastened the blooming period of many mass-flowering crops, which aggravated the floral resource shortage across the landscape. However, the supplementation of honey bee hives in the landscape counteracted the positive effect of flower strips on bumble bee queens. I therefore recommend that the supplementation of honey bee hives should be avoided in landscapes with scarce floral resources to alleviate resource competition between managed and wild pollinators. **I argue that my results provide novel and important insights into the efficiency of flower strips during an extreme weather event associated to climate change. In order to understand the effectiveness of agri-environmental schemes under climate change, I recommend that we need to synthesise results from experiments assessing agri-environmental schemes on biodiversity that were conducted under variable weather extremes that represent future climate predictions.**

With respect to crop production, I confirmed, using pollinator exclusion experiments, that insect pollination is essential to maximise crop yield (paper I, II, IV). My results provide new insights into the complex interactions among insect pollination, land use and other biotic and abiotic conditions. I demonstrate that insect pollination is particularly important in closing yield gaps in fields located in landscapes with low proportions of SNH (paper I). Furthermore, insect pollination enhanced yield independent of water stress and insect herbivory (paper IV). However, supplementing flowering faba bean fields with honey bee hives, which is a common practice to boost crop pollination, did not increase the pollination benefit between bagged and open pollinated plants (paper II). Honey bee hives, if anything, suppressed the pollination potential of wild bumble bees for subsequent growing seasons by weakening the positive effect of flower strips on bumble bee queen abundance (paper III). The fact that higher pollinator densities did not influence the pollination benefit for yield components, suggests that crop plants in our study landscapes were not pollination limited. Yet, wild pollinator populations are continuously declining due to agricultural intensification and climate change (Warren et al., 2018; Zattara and Aizen, 2021). Therefore, agricultural landscapes that are not pollination limited today, might be so in a few years if pollinator densities continue to decline, or during heat waves which momentarily impact pollinator populations (Vanderplanck et al., 2019). It is therefore essential that we manage agricultural landscapes such that they sustain wild pollinator densities. Even if agri-environmental schemes such as higher landscape crop diversity and sown annual flower strips do not show immediate benefits for crop production, they might be key to bolstering crop production in the long-term. **Following on from my thesis results, I recommend future work to assess the pollination benefit in crops over multiple growing seasons in landscapes with variable crop diversity, and with and without flower strips and honey bee hives, alongside continuous monitoring of wild pollinators in the landscapes. Such an experiment would reveal if the legacy effect of diversification measures at different scales can promote wild pollinator population growth and eventually enhance crop production.**

In the light of climate change, I show that large yield gains can only be attained when climate change stressors – in this case water stress and insect herbivory – are reduced simultaneously (paper IV). Yield gain was

negligible in plants that were well-watered but under aphid herbivory compared with water-stressed plants under aphid herbivory. Since water resources are limited, I recommend that water withdrawal for agricultural irrigation is prioritised in crops with high levels of herbivore control. Agricultural landscapes should thus provide the resources required to maintain a species rich and abundant community of natural enemies of pests that provide resilient protection against herbivore outbreaks. Our results confirmed that annual flower strips are particularly successful in attracting a more numerous and diverse community of ground-dwelling predators of pests into crop fields (paper II). Further, I discovered that honey bee hives promoted ladybird beetles (paper II). I found, however, no evidence that more numerous and diverse predator communities translated into enhanced pest suppression or crop yield. **Considering the importance of insect herbivore control under climate change, future research should focus on identifying the factors that determine under what circumstances increased natural enemy communities translate into increased pest control and which do not. As well as to assess interactions among different ecosystem services and biotic stressors under a variety of precipitation and temperature regimes.**

Sustainable crop production requires yield stability, which ensues intact and diverse ecological functions that are robust against climate change stressors. My thesis contributes empirical evidence that access to continuous and diverse floral and shelter resources across agroecosystems is key to support beneficial arthropod communities that can buffer crop production against negative impacts from climate change. Two of my field seasons were unfolding under extreme weather events associated to climate change. In 2017, weather conditions were unusually wet and cold, while 2018 was extremely hot and dry. Perhaps it is difficult to make general predictions from these results. Yet, I argue that my thesis offers valuable insight into how effective diversification strategies are under climate change. Finally, I moved on to incorporate “my weather luck” into my final field season in 2019 by including the experienced and anticipated climate change risks into a carefully designed experiment. **In order to understand the mechanisms underlying ecosystem interactions, and to make better predictions for crop production under land use and climate change, I believe that we need a combination of mechanistic and modelling research approaches.**

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Popular science summary

How do we feed a growing and wealthier world population without sacrificing the planet's well-being and the diversity of life forms we have today? This question has concerned humans for decades and remains one of the greatest challenges of our time.

Over the past sixty years, modern technology succeeded in producing more food on the same amount of land and in doing so drastically reduced the number of people left hungry. However, the paradigm of intensive agriculture sees humans and nature as antagonists, and the success of producing more food is largely due to the adoption of technologies to kill undesired natural actors such as insects eating crops, diseases or weeds. But intensive agriculture did not just combat organisms in crop fields, no it transformed entire landscapes. The traditional agricultural landscapes that were characterised by mosaics of small fields, flower-rich meadows and forest patches had to make way to expanding fields with monocultures of few crop types that dominate entire landscapes. Such simplified landscapes provide very few opportunities for organisms such as insects to nest, find shelter or food resources, all of which are essential for them to survive and reproduce.

During spring, yellow seas of oilseed rape provide an abundance of nectar and pollen for insects to feast on, but within a few weeks bloom is over leaving its flower visitors left hovering in front of empty plates. In addition to these land use changes, climate change is also negatively impacting many insects. For example, extreme weather events such as droughts and heat waves shorten the flowering time of crops and wild plants and so reduce food availability even further. As a consequence, insect populations have been plummeting over the past decades in both numbers and species diversity. With every species or population that

disappears, interactions with other species are eroded risking the loss of ecosystem services – functions provided by nature that benefit us humans. Ironically, some of these ecosystem services, such as pollination, pest regulation or nutrient cycling, are pivotal for agriculture, and the loss of biodiversity and ecosystem services have started to take its toll in some regions by making crop yields more unstable.

Crop yield stability is also increasingly impacted by climate change stressors. Extreme weather events subject crops to water or heat stress, and warming climates increase the consumption rates of insect herbivores, which can lead to pest outbreaks if their numbers are not regulated in time. Taken together, sustainable agricultural systems that work together with nature – not against it – are urgently needed to bolster crop production in the face of global change.

Ecological intensification of agriculture seeks to intensify and diversify the functions of nature to produce more food. Diverse flower, shelter and nesting resources are integrated into agricultural landscapes to provide pollinators and predators of pests with the resources they need to fulfil their lifecycles and facilitate their movement between habitat patches to find mates and establish new populations. In my thesis, I assessed how such diversification strategies, at landscape and field scale, affect insect and spider communities, and how these changes in community composition translate into ecosystem services delivered to crop fields. More so, I was interested in setting up an experiment that tests how insect pollination is affected by climate change stressors. Specifically I asked i) can landscapes with more forest and pasture patches or more diverse crop types benefit pollinators, insect pollination of crop flowers and crop yield? ii) how do flower strips sown along field edges influence the communities of beneficial insects and pests in the crop and the wider landscape, and how are these effects impacted when honey bee hives are added, which potentially compete with wild insects for resources? iii) how do flower strips and honey bee hives influence ecosystem services and crop yield? iv) how does the insect pollination benefit get impacted by simultaneous water stress and insect herbivory, stressors that are expected to occur more frequently under climate change? I used faba bean cropping as a model system to answer these questions.

I found that landscapes with a higher diversity of crop types and with more forest patches and pastures enhanced bumble bee densities in faba

bean fields. Flower strips enhanced carabid beetle species diversity and spider abundance in the strip and in the faba bean fields, probably by providing these ground predators with shelter habitat. Flower strips did not attract more bumble bees from the landscape to the faba bean field. However, flower strips did enhance bumble bee queen abundances in the landscape the following spring, but this positive effects of flower strips was lost in landscapes with many honey bee hives. I propose that both the failure of flower strips to attract more bumble bees into faba bean fields, and the significant positive effect of flower strips on bumble bee queen abundances in the landscape the following spring were in part driven by the unusually hot and dry summer in 2018. Due to the extreme weather, the flower strip and faba bean blooming period barely overlapped, and so the additional floral resources provided by the flower strip might not have been sufficient to attract more bumble bees from the wider landscape. In contrast, the nectar and pollen provided by the flower strip in late summer were particularly needed by bumble bees because the hot and dry weather hastened the bloom of many flowering crops, which starved the bees in late summer even more than usual. Faba bean yield was higher in insect pollinated compared with self-pollinated plants but the insect pollination benefit reduced with increasing proportions of forest and pasture patches in the landscape, but was independent of water stress and insect herbivory. Honey bee hive supplementation did not boost yield but enhanced aphid and ladybird beetle densities. Faba bean yield was higher in landscapes with more forests and pastures, but this effect were not driven by pollinator numbers but factors we did not measure. Finally, yield losses can be greatly reduced when climate change stressors, such as water stress and insect herbivory, are reduced simultaneously. Instead, minimal yield gains were realised when water stress was alleviated but plants were under insect herbivore attack.

My thesis shows, using observations and realistic experiments, that access to continuous and diverse floral and shelter resources across agricultural landscapes are key to support beneficial insect communities that are needed for crop production, particularly under climate change. Two of my field seasons were unfolding under extreme weather events associated to climate change. In 2017, weather conditions were unusually wet and cold, while 2018 measured the hottest and driest summer on record. You might be wondering if results that are collected under such

unusual conditions can be used to make general conclusions. I argue that my thesis offers valuable insight into how crop diversity and flower strips work under weather conditions that might soon become the norm given climate change. Based on my results, I recommend that farmers and landowners are encouraged and supported to include more crops into crop rotations to increase landscape crop diversity, and to sow flower strips, both of which provide extra food and shelter habitats in agricultural landscapes. In addition, remaining forest and grassland patches should be retained as important nesting and foraging habitats. I recommend that the supplementation of honey bee hives should be avoided in landscapes with scarce floral resources to avoid resource competition between managed and wild pollinators. I also recommend that water withdrawal for agricultural irrigation is prioritised in crops, which are free from herbivores. Agricultural landscapes should provide the resources required to maintain a diversity of pollinators, and of natural enemies of pests that provide resilient protection against herbivore outbreaks.

Populärvetenskaplig sammanfattning

Hur ska vi möta efterfrågan på mat till en ökande världsbefolkning med ökat välstånd utan att hota planetens välbefinnande och den mångfald av livsformer vi har idag? Denna fråga har berört människor i årtionden och är fortfarande en av vår tids största utmaningar.

Under de senaste sextio åren har modern teknik lyckats producera mer mat på samma mängd mark och därmed drastiskt minskat antalet människor som lever i hunger. Paradigmet för intensivt jordbruk ser emellertid människor och natur som antagonister, och framgången med att producera mer mat beror till stor del på tillämpningen av teknik för att döda oönskade besökare i grödan, som växtätare, växtsjukdomar eller ogräs. Men intensivt jordbruk bekämpar inte bara organismer i åkern, utan har förvandlat hela landskap. De traditionella jordbrukslandskapen som kännetecknades av en mosaik av små åkrar, betesmarker och skogsdungar har ersatts av expanderande åkrar där ett fåtal grödor odlas i monokulturer som dominerar hela landskapet. Sådana likformiga landskap ger mycket få möjligheter för organismer att hitta boplatser, skydd eller föda, som är nödvändigt för dem att överleva och reproducera.

Under våren ger gula hav av raps ett överflöd av nektar och pollen för insekter att festa på, men inom några veckor är blomningen över och fältets besökare får lämna igen, tomhänta. Förutom dessa förändringar i markanvändningen påverkar klimatförändringar också många organismer negativt. Extrema väderhändelser som torka och värmeböljor förkortar blomningstiden för grödor och vilda växter och minskar därmed matresurserna ytterligare. Som en konsekvens har insektspopulationer minskat under de senaste decennierna i både antal och mångfald. För varje art eller population som försvinner, urholkas samspelet mellan arter och vi riskerar förlust av ekosystemtjänster - funktioner som tillhandahålls av

naturen och som gynnar oss människor. Ironiskt nog är några av dessa ekosystemtjänster, som pollinering, kontroll av skadegörare eller näringscykling, avgörande för jordbruket, och förlusten av biologisk mångfald och ekosystemtjänster har börjat synas i vissa regioner genom mer instabila skördar.

Grödans skörde stabilitet påverkas också alltmer av klimatförändringar. Extrema väderförhållanden utsätter grödor för vatten- eller värmestress, och det varmare klimatet ökar de växtätande insekternas aptit, vilket kan leda till skadedjursutbrott om deras antal inte regleras i tid. Sammantaget behövs det hållbara system för jordbruk som arbetar tillsammans med naturen - inte i kamp mot den - för att stärka jordbruksproduktionen vid förändringar i klimat och miljö.

Ekologisk intensifiering av jordbruket försöker intensifiera och diversifiera naturens funktioner för att producera mer mat. En mångfald av blomresurser, skydd och boplatser integreras i jordbrukslandskapet för att ge pollinerare och skadedjurens naturliga fiender de resurser de behöver för att fullfölja sina livscyklar och underlätta deras rörelse mellan livsmiljöer för att hitta artfränder, para sig och etablera nya populationer. I min avhandling undersökte jag hur sådana diversifieringsstrategier, på landskaps- och fältnivå, påverkar insekts- och spindelsamhällen och hur dessa förändringar i samhällssammansättningen översätts till ekosystemtjänster som levereras till grödor. Jag var också intresserad av att skapa ett experiment som testar hur insektspollinering påverkas av stressfaktorer kopplade till klimatförändring. Specifikt frågade jag i) om landskap med mer skogsdungar och betesmarker eller en högre mångfald av olika grödor kan gynna pollinerare, insektspollinering av grödan och skörden? ii) hur påverkar blomremсор sådda längs fältkanterna insektsamhällen i grödan och i landskapet och hur påverkas dessa effekter av utsättning av honungsbikupor, som potentiellt konkurrerar med vilda insekter om resurser? iii) hur påverkar blomremсор och honungsbikupor ekosystemtjänster och skörd? iv) hur påverkas nyttan av insektspollinering av samtidig stress till följd av vattenbrist och insektsätare, stressfaktorer som förväntas förekomma oftare under klimatförändringar? Jag använde odling av åkerböna som ett modellsystem för att svara på dessa frågor.

Jag fann att landskap med en ökad mångfald av grödtyper och med fler skogsdungar och betesmarker ökade antalet humlor i åkerbönsfält. Blomremсор ökade jordlöparens mångfald och antalet spindlar i remsan och i

åkerbönsfält, troligen genom att ge dessa marklevande rovdjur en skyddande miljö. Blomremсор lockade inte fler humlor från landskapet till åkerbönsfält. Blomremсор ökade dock antalet humledrottningar i landskapet följande vår, men de positiva effekterna av blomremсор förlorades i landskap med många honungsbikupor. Jag föreslår att både att blomremсорna inte lyckades locka fler humlor till åkerbönsfälten och den positiva effekten av blomremсор på humledrottningar i landskapet våren efter delvis drevs av den ovanligt varma och torra sommaren 2018. På grund av det extrema vädret överlappade blomningen av blomremсорna och åkerbönsorna knappt och därför var de extra blomresurserna från blomremсорna kanske inte tillräckliga för att locka fler humlor från landskapet. Däremot var behovet av nektar och pollen från blomremсорna på sensommaren extra stort hos humlorna eftersom det varma och torra vädret påskyndade blomningen av många grödor, vilket ledde att humlorna mer än vanligt led av svält under sensommaren. Insektspollinerade åkerbönsor gav högre skörd och nyttan av insektspollinering minskade med andelen skog och betesmarker i landskapet, men var oberoende av vattenstress och förekomst av växtätande insekter. Tillskott av honungsbisamhällen ökade inte skörden men ökade antalet bladlöss och nyckelpigor. Åkerbönskoröden var högre i landskap med mer skog och betesmarker, men dessa effekter drevs inte av antal pollinere utan faktorer som vi inte mätte. Slutligen kan skördeförluster minskas kraftigt när stressfaktorer från klimatförändringar, som vattenbrist och växtätande insekter, minskas samtidigt. Istället uppnåddes minimala skördevinster när vattenbristen lindrades men växterna fortfarande var angripna av bladlöss.

Min avhandling visar med hjälp av observationer och realistiska experiment att tillgång till kontinuerliga och varierande födoresurser och skydd i jordbrukslandskap är nyckeln till att stödja samhällen av nyttoinsekter som behövs för grödproduktion, särskilt under klimatförändringar. Två av mina fältsäsonger utspelade sig under extrema väderhändelser kopplade till klimatförändringar. 2017 var ovanligt våt och kall, medan sommaren 2018 var rekordmässigt het och torr. Du kanske undrar om resultat som samlas in under sådana ovanliga förhållanden kan användas för att dra generella slutsatser. Jag hävdar att min avhandling ger värdefull inblick i hur gröddiversitet och blomremсор fungerar under väderförhållanden som snart kan bli normen med tanke på klimatförändringen. Baserat på mina resultat rekommenderar jag att bönder

och markägare uppmuntras och stöds för att inkludera fler grödor i växtföljden för att öka mångfalden i landskapet och att så blomremor, vilka båda ger extra mat och skyddsmiljöer i jordbrukslandskap. Dessutom bör kvarvarande skogsdungar och betesmarker behållas som viktiga boplats- och födosöksmiljöer. Jag rekommenderar att honungsbikupor undviks i landskap med brist på blomresurser för att undvika resurskonkurrens mellan tambin och vilda pollinerare. Vidare rekommenderar jag att bevattning prioriteras till grödor som är fria från växtätande insekter. Jordbrukslandskap bör tillhandahålla de resurser som krävs för att upprätthålla en mångfald av pollinerare och naturliga fiender som ger ett resilient skydd mot utbrott av växtätande insekter.

Populärwissenschaftliche Zusammenfassung

Wie können wir eine wachsende und immer wohlhabendere Weltbevölkerung ernähren, ohne dabei das Wohl unseres Planeten und die Vielfalt heutiger Lebensformen zu opfern? Diese Frage beschäftigt die Menschheit seit Jahrzehnten und bleibt eine der größten Herausforderungen unserer Zeit.

In den letzten sechzig Jahren ist es dank modernen Technologien gelungen, mehr Nahrungsmittel auf der gleichen Fläche zu produzieren und damit den Welthunger drastisch zu reduzieren. Das Paradigma der intensiven Landwirtschaft sieht jedoch Mensch und Natur als Gegenspieler. Die gesteigerte Nahrungsmittelproduktion ist größtenteils auf die Einführung von Technologien zurückzuführen, die unerwünschte natürliche Akteure wie Schädlinge, Pflanzenkrankheiten oder Unkraut bekämpfen. Doch die intensive Landwirtschaft bekämpft nicht nur unerwünschte Organismen auf den Äckern, sie verändert auch ganze Landschaften. Die traditionellen Agrarlandschaften, die von einem Mosaik aus kleinen Feldern, blumenreichen Wiesen und Waldstücken geprägt waren, mussten ausgedehnten Feldern mit Monokulturen weniger Kulturpflanzen weichen. Solch eintönige Landschaften bieten Lebewesen nur wenige Möglichkeiten zu nisten oder Unterschlupf und ausreichend Nahrung zu finden, allesamt unerlässlich für das Überleben einer Art.

Im Frühjahr bieten gelbe Meere aus Rapsblüten eine Fülle von Nektar und Pollen für Insekten zum Schlemmen an, aber innerhalb weniger Wochen ist die Blüte vorbei und die Blütenbesucher schweben vor leeren Tellern. Neben diesen Veränderungen in der Landnutzung wirkt sich auch der Klimawandel auf viele Organismen negativ aus. Zum Beispiel verkürzen extreme Wetterereignisse wie Dürren und Hitzewellen die Blütezeit von Kultur- und Wildpflanzen und verknappen so das Nahrungsangebot weiter. Als Folge davon sind in den letzten Jahrzehnten Insektenpopulationen drastisch zurückgegangen. Mit jeder Art oder

Population, die verschwindet, können auch Interaktionen mit anderen Arten nicht mehr stattfinden und es besteht die Gefahr, dass Ökosystemleistungen verloren gehen - Funktionen, die von der Natur bereitgestellt werden und uns Menschen zugute kommen. Ironischerweise sind einige dieser Ökosystemleistungen, wie z. B. die Bestäubung von Kulturpflanzen, die Schädlingsregulierung oder der Nährstoffkreislauf, für die Landwirtschaft von zentraler Bedeutung. Der Verlust der biologischen Vielfalt und damit einher der Ökosystemleistungen hat in einigen Regionen bereits seinen Tribut gefordert, und instabile Ernteerträge verursacht.

Die Stabilität der Ernteerträge wird zunehmend auch durch den Klimawandel beeinträchtigt. Extreme Wetterereignisse setzen Nutzpflanzen Wasser- oder Hitzestress aus, und die Klimaerwärmung erhöht den Verzehr durch pflanzenfressende Insekten. Wenn deren Anzahl nicht rechtzeitig reguliert wird, sind Schädlingsausbrüche die Folge. Um die landwirtschaftlichen Erträge angesichts des globalen Wandels zu sichern sind nachhaltige landwirtschaftliche Systeme, die mit statt gegen die Natur arbeiten, dringend erforderlich.

Die gesteigerte Ökologisierung der Landwirtschaft zielt darauf ab, die Funktionen der Natur zu fördern. Vielfältige Blüten-, Unterschlupf- und Nistressourcen werden in die Agrarlandschaften integriert, um Bestäubern und anderen Nützlingen alles Nötige zur Erfüllung ihres Lebenszyklus zur Verfügung zu stellen. So werden auch Bewegungskorridore zwischen den Lebensraumtypen angelegt, damit Paarungspartner gefunden und neue Populationen gegründet werden können. In meiner Dissertation habe ich untersucht, wie sich in der Landschaft allgemein und auf Feldern im Besonderen solche Diversifizierungsstrategien auf Insekten und Spinnen auswirken. Weiter habe ich untersucht, wie sich diese Veränderungen auf die Ökosystemleistungen auswirken. Darüber hinaus habe ich getestet ob und wie die Bestäubung durch Insekten vom Klimawandel beeinflusst wird. Konkret verfolgte ich die Fragen: i) Können Landschaften mit mehr Wald- und Wiesenflächen oder vielfältigeren Kulturpflanzenarten den Bestäubern, der Insektenbestäubung von Kulturpflanzen und dem Ernteertrag zugute kommen? ii) Wie beeinflussen Blühstreifen entlang der Felder Nützlinge und Schädlinge, und wie werden diese Effekte beeinflusst, wenn Honigbienenstöcke hinzugefügt werden, die potentiell mit wilden Insekten um Ressourcen konkurrieren? iii) Wie beeinflussen Blühstreifen und Bienenstöcke die Ökosystemleistungen und den Ernteertrag? iv) Wie wird

der Nutzen der Insektenbestäubung durch gleichzeitigen Wasserstress und pflanzenfressende Insekten beeinflusst, Stressfaktoren, die angesichts des Klimawandels häufiger auftreten werden? Um diese Fragen zu beantworten, habe ich die Ackerbohnenproduktion als Modellsystem verwendet.

Meine Erhebungen haben gezeigt, dass Landschaften mit einer höheren Vielfalt an Kulturpflanzen und mit mehr naturnahen Lebensräumen Hummeln in Ackerbohnenfeldern positiv beeinflussen. Blühstreifen förderten die Artenvielfalt von Laufkäfern und die Vielzahl an Spinnen in den Blühstreifen sowie in den angrenzenden Ackerbohnenfeldern, wahrscheinlich weil sie diesen am Boden lebenden Räubern Deckung und ein besseres Kleinklima bieten. Im Gegenzug lockten Blühstreifen nicht mehr Hummeln zu den Ackerbohnenfeldern. Allerdings förderten Blühstreifen im darauffolgenden Frühjahr die Anzahl von Hummelköniginnen in der Umgebung. Dieser positive Effekt der Blühstreifen wurde jedoch in Landschaften mit vielen Honigbienenstöcken reduziert. Ich vermute, dass sowohl der Misserfolg, mit Blühstreifen mehr Hummeln in die Ackerbohnenfelder zu locken, als auch der positive Effekt von Blühstreifen auf die Anzahl Hummelköniginnen in der Landschaft im darauffolgenden Frühjahr zumindest teilweise durch den ungewöhnlich heißen und trockenen Sommer 2018 verursacht wurden. Aufgrund des extremen Wetters überlappten sich die Blütezeit von Blühstreifen und Ackerbohnenfeldern kaum, sodass die zusätzlichen Nektar- und Pollenressourcen des Blühstreifens möglicherweise nicht ausreichten, um mehr Hummeln aus der umgebenden Landschaft anzulocken. Im Gegensatz dazu wurden die Nektar- und Pollenressourcen des Blühstreifens im Spätsommer besonders von Hummeln benötigt, da das heiße und trockene Wetter die Blüte vieler Kulturpflanzen verkürzte und so die vorhandenen Futterressourcen noch mehr als gewöhnlich beeinträchtigt waren. Der Ertrag von Ackerbohnen war bei den von Insekten bestäubten Pflanzen höher als in selbstbefruchteten Pflanzen. Dieser durch die Insektenbestäubung erzielter Ertragsgewinn war aber geringer in Landschaften mit höherem Anteil an naturnahen Lebensräumen, jedoch unabhängig von Wassermangel und Blattlausbefall. Bienenstöcke, die entlang der Felder aufgestellt wurden, steigerten den Ackerbohnenenertrag nicht, erhöhten jedoch die Anzahl von Blattläusen und Marienkäfern. Der Ertrag von Ackerbohnen war in Landschaften mit mehr naturnahen

Lebensräumen höher, aber dieser Effekt wurde nicht durch die Anzahl der Bestäuber bestimmt, sondern durch andere Faktoren, die sich uns bisher nicht erschlossen haben. Ertragsverluste konnten stark reduziert werden, wenn die Stressfaktoren des Klimawandels wie Wassermangel und Insektenfrass gleichzeitig reduziert wurden. Hingegen wurden nur minimale Ertragsgewinne erzielt, wenn ausreichend Wasser zur Verfügung stand, die Pflanzen aber weiterhin von Blattläusen befallen waren.

Meine Dissertation zeigt anhand von Beobachtungen und praxisnahen Experimenten, dass kontinuierliche und vielfältige Blumen- und Lebensraumressourcen in Agrarlandschaften der Schlüssel zur Unterstützung nützlicher Insektengemeinschaften sind, die für die Pflanzenproduktion insbesondere unter dem Einfluss des Klimawandels benötigt werden. Während zwei meiner drei Untersuchungsperioden herrschten extreme Wetterbedingungen: Im Jahr 2017 war das Wetter ungewöhnlich nass und kalt, während im Jahr 2018 der Sommer einer der heißesten und trockensten seit Messbeginn war. Man kann sich fragen, ob Daten, die unter solch aussergewöhnlichen Bedingungen erhoben wurden, für allgemeine Schlussfolgerungen verwendet werden können. Angesichts des Klimawandels werden solche klimatischen Bedingungen aber wohl zur Norm werden. Daher ermöglicht meine Dissertation wertvolle Einblicke in die Funktionsweise vielfältiger Kulturlandschaften und Blühstreifen unter extremen Wetterbedingungen.

Basierend auf meinen Ergebnissen empfehle ich, dass Landwirte und Landbesitzer ermutigt und unterstützt werden, mehr Blühstreifen zu säen und mehr Kulturen in Fruchtfolgeflächen anzubauen, um die Vielfalt der Anbaukulturen zu erhöhen. Darüber hinaus sollten verbleibende Wald- und Wiesenflächen als wichtige Nist- und Nahrungslebensräume erhalten bleiben. Ich empfehle in Landschaften, die nur wenige Blütenpflanzen aufweisen, keine Bienenstöcke aufzustellen, um einen Ressourcenwettbewerb zwischen wilden Bestäubern und Honigbienen um Nektar und Pollen zu vermeiden. Weiter empfehle ich, dass die Bewässerung von Kulturpflanzen ausschliesslich auf Feldern vorgenommen wird, die nicht von Blattläusen befallen sind. Agrarlandschaften sollten alle Ressourcen bereitstellen, die das Gedeihen einer Vielzahl von Bestäubern und natürlichen Feinden ermöglichen, insbesondere im Zuge des Klimawandels.

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Land use and climate change impact arthropod communities in agroecosystems and threaten the supply of ecosystem services such as pollination and biological pest control, and crop yield stability. My research has documented how diversification strategies at field and landscape scale can benefit arthropod communities and ecosystem services in agroecosystems using faba bean cropping as a model system. The results are particularly relevant in the light of safeguarding sustainable crop production under climate change.

Chloë Aline Raderschall received her PhD education from the Department of Ecology, SLU in Uppsala, and obtained her BSc Hons and MPhil degrees from the Research School of Biology at the Australian National University in Canberra.

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