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Multi-level trophic interactions in diversified cropping systems

Functioning and dynamics among above- and belowground arthropods

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Cover: Carabid predators in arable field
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Multi-level trophic interactions in diversified cropping systems

Abstract

Cropping practices alter the occurrence and abundance of species, and their interactions, in agricultural fields. Such alterations can impede the delivery of ecosystem functions by disrupting processes that would otherwise nourish and protect the crops. I examine how single and combined diversification practices of lowering tillage intensity or including perennial leys in crop rotations with or without amendment of organic fertiliser affect predatory ground beetles, herbivores, and soil fauna within and across crop growing seasons. I examined the effects of changes in coupled above- and belowground communities on predator-prey interactions, focusing on consequences for biological pest regulation. Molecular gut content analysis of what predators had eaten demonstrated that species rich predator communities strengthen pest regulation through predators' trophic redundancy. Increased tillage intensity decreased the abundance of soil mesofauna, resulting in resource discontinuity for predators relying on soil fauna as alternative prey early in the crop growing season. I discovered that communities of above- and belowground arthropods are inextricably linked in time, and that arthropods benefit from habitat continuity and increased structural complexity of arable habitats. However, the recovery and recolonisation after disturbance was only marginally linked to predator overwintering within arable fields. Although results vary across diversification practices and temporal scales examined in this thesis, I identified habitat and resource continuity across the growing season as a key property of diversified management that bolsters predatory and soil arthropods. Variable effects found across taxa emphasise the need to focus on species ecology, and to put effort into identifying ecological linkages across species. By this approach, we can understand the impact of management on ecosystem functions derived from these communities.

Keywords: beneficial arthropods, temporal dynamics, diversified management, tillage, organic fertiliser, perennial ley

Trofiska interaktioner på flera nivåer i diversifierade odlingssystem

Sammanfattning

Olika jordbruksmetoder påverkar förekomsten och mängden av arter i åkrar, samt hur dessa arter växelverkar med varandra. Sådana påverkningar kan också komma att motverka ekosystemfunktioner som annars skulle främja och skydda grödan. I denna avhandling undersöker jag hur diversifieringsmetoder inom jordbruket, enskilt eller i kombination av minskad plöjintensitet eller införande av perenna vallar i växtföljder med eller utan tillförsel av stallgödsel påverkar marklevande skalbaggar, herbivorer och markfauna inom och över flera växtsäsonger. Jag granskar även effekterna av förändringar i biologiska samhällen ovan- och under jord växelverkan mellan rovdjur och byten, med fokus på konsekvenser för biologisk skadedjursbekämpning. Molekylära analyser av predatorers maginnehåll visade att artrika predatorsamhällen ökar skadedjursreglering genom trofisk redundans. Ökad jordbearbetning minskade antalet markmesofauna och ledde till brist på födokontinuitet för predatorer som är beroende av markfauna som alternativ föda tidigt under växtsäsongen. Jag upptäckte att leddjurssamhällen ovan- och under jord är sammanlänkade över tiden, samt att dessa samhällen främjas av kontinuitet och ökad strukturell komplexitet i åkerhabitaten. Återhämtning och återkolonisering efter markstörning var dock endast marginellt knuten till predatorers övervintrande i åkermark. Trots att resultaten visar på variation i effekterna av de diversifieringstekniker och tidsperspektiv som undersöks i avhandlingen, så påvisar jag samtidigt att habitat- och födokontinuitet genom växtsäsongen är en nyckelaspekt då man vill främja leddjurssamhällen genom ett diversifierat lantbruk. Variationen mellan arterna understryker vikten av ekologi bedriven på artsnivå, och visar att mer fokus måste läggas på att identifiera och förstå sambandet mellan arter. Genom dessa tillvägagångssätt kan vi bättre förstå hur jordbruksmetoder påverkar de ekosystemfunktioner som åkrarnas organismsamhällen tillhandahåller.

Nyckelord: Nyttiga artropoder, temporal dynamik, diversifierade jordbrukstekniker, plöjning, gödsel, perenna vallar

Dedication

To my sister. You can achieve everything you want; be fearless!

> *Not everything that can be counted counts, and not everything that counts can be counted.*–Albert Einstein

Contents

List of publications

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

I. Heinen, J., Smith, M.E., Taylor, A., Bommarco, R. (2023). Combining organic fertilisation and perennial crops in the rotation enhances arthropod communities. *Agriculture, Ecosystems and Environment*, 349:108461.

II. Heinen, J., Bommarco, R., Taylor, A., Viketoft, M., Lundin, O., Emery, S. Decreased tillage intensity enhances soil mesofauna and ground dwelling arthropod predators differently. (manuscript)

III. Heinen, J., Dominguez, V., Aguilera, G., Vesterinen, E., Roslin, T. Bommarco, R. and Bartomeus, I. Agricultural diversification builds species rich predator communities which strengthens herbivore regulation *via* predators' trophic redundancy. (submitted manuscript)

IV. Heinen, J., Smith, M.E., Lundin, O., Bommarco, R. Within-field predator overwintering supply assemblages in arable fields, irrespective of tillage intensity. (manuscript)

The contribution of Janina Heinen to the papers included in this thesis was as follows:

I. Main author. JH planned and designed the experiment with the co-authors. JH supervised and conducted the field work with help from MES. JH analysed the data, interpreted the results and wrote the manuscript with supervision of MES and RB. All authors commented on the final version of the manuscript.

II. Main author. OL and SE designed the experiment with help from AT and MV. JH and SE supervised and conducted fieldwork. JH analysed the data, interpreted the results and led the writing of the manuscript. All authors contributed to the manuscript preparation.

III. Main author. JH and RB planned and designed the experiment. JH and GM collected the data and EV performed genetic sequencing. JH, VD, GA and IB conceptualised the analysis. JH analysed the data and led the writing of the manuscript under supervision of IB and VD. All authors contributed to the manuscript preparation.

IV. Main author. JH& RB planned and designed the experiment. JH supervised and conducted fieldwork on experimental sites selected by OL. MES analysed the data. JH wrote the manuscript with input from RB, MES and OL.

Abbreviations

COI	Mitochondrial cytochrome oxidase I gene
zOTU	Zero-radius Operational Taxonomic Unit
WOSR	Winter oil seed rape
SOM	Soil organic matter
EU	European Union

1. Introduction

There are several long standing questions in ecology that are especially pertinent when considering agroecosystems, where ecological theory meets applied relevance. To understand the drivers of ecosystems we must investigate what determines the population size of different organisms in communities, why certain places (fields) are more diverse than others, and how diversity eventually affects the functioning of ecosystems.

In agroecosystems, the population size and dynamics, are too large extends, shaped by agricultural management. Depending on whether organisms thrive or decline under such management, can have consequences for crop production and food provisioning. In general, loss of biodiversity in agroecosystems can impair biodiversity-mediated functions and consequently limit crop yields. Despite the recognition that species population size, community dynamics, and configuration of communities are critical for sustainable crop production, their intrinsic linkages are not well understood. In my thesis, I explore the effect of diversified agricultural management on arthropod communities within arable fields. I illustrate the ecological consequences of agricultural management on arthropods, within the frame of sustainable cropping systems, by specifically addressing communities' linkages in time and across the above- and belowground interface.

1.1 Relation between agricultural management practices and biodiversity in arable fields

Arable fields host a large variety of species above- and belowground whose habitats are repeatedly disturbed by agricultural management. Belowground communities are diverse, encompassing millions of species across different taxon groups and their complex interactions (Bardgett & Van Der Putten, 2014). For example, earthworms, ingest organic materials, and though burrowing activities, aid in bioturbation of soils, creating structural habitat complexity and facilitate the distribution of organic materials throughout the soil horizon (Lavelle et al., 1997). Smaller bodied species such as collembolans, shred organic materials further, aiding the breakdown of organic materials and subsequently release nutrients to the crops (Pamminger et al., 2021). The consequences of biodiversity loss on soil functions are universal across biomes (Handa et al., 2014; Pamminger et al., 2021). In agroecosystems, this has applied relevance for the sustainable provision of nutrients to crops. Furthermore, soil functions derived from the complexity and configuration of interactions have cascading effects on aboveground crop primary production (Laakso & Setala, 1999; Wardle et al., 2004), but also affect pest regulation, as many soil organisms constitute prey to higher trophic levels, such as birds and arthropod predators.

Aboveground communities are comprised of a multitude of taxa, which play the roles of predators, pollinators, parasitoids and herbivores, a few of which can be pests (Lohaus et al., 2013). Pollinators can boost crop yields by increasing pollination (Raderschall et al., 2021). Arthropod predators such as carabids, spiders and staphylinids can exert top-down predation pressure on herbivorous crop pests and manage their population densities *via* their intricate trophic interactions (Bellone et al., 2023).

1.1.1 Challenges for sustainable agriculture: transition from agricultural- to ecological intensification

Agricultural management, has exacerbated biodiversity loss through the ongoing intensification of practices, and stripped away arthropods ability to live in and from arable land (Kehoe et al., 2017; Smith & Mortensen, 2017) creating several challenges for sustainable agriculture. Current cropping systems are highly productive, and have succeeded in increasing yields over the last decades, but the system is heavily reliant on external inputs of fertiliser and pesticides (Tilman et al., 2002; Pingali, 2012). Processes such as nutrient cycling and pest regulation, which in natural ecosystems are generated by interactions within diverse communities, are progressively lost and replaced by further human interventions (Tilman et al., 2002; Foley et al., 2005). Especially, the use of pesticides to regulate pest pressures on crops has led to unprecedented biodiversity loss in agroecosystems (EEA, 2019) and prompted the European Union (EU) to ban several agrochemicals. Specifically, the implemented "farm to fork strategy" intends to cut the use and risk of chemical pesticides by at least 50% by 2030 (EC, 2020b).

Restoring the biodiversity in agroecosystems is the key challenge for transitioning from current, to more sustainable cropping systems. Such ecological intensification is based off adapting management practices to improve crop productivity though enhancing biodiversity mediated ecosystem services in order to replace external inputs. Thus, ecological intensification contrasts the high impact, high input farming practices, yet is effective in supporting yields (Bommarco et al., 2013; Tittonell, 2014). By relying on biodiversity mediated processes in cropping systems, the yield gap, i.e. the difference between the actual and potential production, could be closed (Van Ittersum & Rabbinge, 1997; Bommarco et al., 2013), alongside decreasing management costs due to fewer field visits and lesser need for costly agrochemicals.

However, current crop production systems lack the necessary features to support biodiversity that would likely increase and stabilise functions supporting crop production. Adapting agricultural management to harness the full potential of biodiverse communities, necessitates a thorough understanding of how management affects species habitats, thus creating potential mismatches between species and their environment.

1.1.2 Within-field diversification practices: a tool to transform arable fields into biodiversity hot-spots?

Providing suitable habitats for species outside the crop fields (i.e. field margins, semi natural habitats) has been the focus for enhancing biodiversity in arable fields (Ramsden et al., 2015; Kremen & Merenlender, 2018; Aguilera et al., 2020). However, biodiversity within fields generates a variety of services, thus management should be adapted to support species within fields. Reduced within-field management can mitigate the negative effects of landscape simplification (Tamburini et al., 2016; Lichtenberg et al., 2017), emphasising its potential to strengthen biodiversity within fields, especially if applied across large areas. Accordingly, fields must be recognised and managed as biodiverse habitats if we are to farm sustainably and conserve biodiversity. Within-field diversification aims at lowering disturbances, and to provide suitable habitat for species but benefits can arise through multitude of impacts on biodiverse communities.

Crop rotation

Crop rotations are the sequences of crops cultivated within arable fields, which are often grown in short rotations of a few high yielding annual crops (Castellazzi et al., 2008; Reckling et al., 2016a). Crop rotation represents one of the main management pillars in agricultural production, with the aim of maintaining soil fertility, breaking pest and disease cycles (i.e. weeds, herbivore pests) (Davis et al., 2012; Dury et al., 2012) and increasing the overall agroecosystem resilience (Lin, 2011; Kollas et al., 2015). Long-term plot trials suggest that rotations with multiple crops benefit yields over time (Smith et al., 2023) which can be ascribed to enhanced soil fertility and nutrient cycling (MacLaren et al., 2022). Studying crop rotations aids our understanding of cumulative effects over time, unravelling legacies that might not be detectable in a single crop (Reckling et al., 2016b). Regardless of the affirmed benefits of diverse rotations, current rotation schemes are narrow. In Sweden, crop rotations are dominated by cereals (wheat, barley, oats) and crop diversity has continuously declined in the last 20 years (Schaak et al., 2023). Conventional systems have usually two break crops within ten year rotations (Reumaux et al., 2023). Growing crops in such simplified rotations created the need for the subsidisation of crops with fertilisers and pesticides. However, with the recent ban of numerous agrochemicals in the EU, a greater need emerged to harness the benefits of rotations. Extending rotations with perennial crops is a new avenue for increasing soil fertility by simultaneously enhancing biodiversity in fields.

Perennial crops

Perennials, as opposed to annual crops, are cultivated for many consecutive years, and are usually cut several times in the crop growing season (Weißhuhn et al., 2017). Perennials are most commonly grown as grass-legume mixes for forage and fodder, from now on referred to as perennial ley (Glover et al., 2010; Asbjornsen et al., 2014), or to a lesser extend as energy crops (Mast et al., 2014; Franzluebbers, 2015). Diversifying or extending crop rotations with perennial ley aims at lowering disturbance while also capitalising on benefits from plant species mixtures with complementary resource use (Picasso et al., 2011). The variety of different plant species grown in perennial leys stands in contrast to single-species annual crops and can increase plant diversity in fields and therefore create abundant soil organic matter (SOM) and nutrient profiles in the soils. Perennial ley thus also has the ability to supress weeds due to competitive effects among weeds and plants in ley mixtures (Sjursen et al., 2012; Suter et al., 2017).

What is more, most associated arthropods rely on habitat and resource continuity that is provided by growing perennial leys. Perennial leys are usually cultivated for 3 to 5 consecutive years, thus increase habitat stability, but also provide arthropods with stable resources, in form of organic matter, throughout time (Scotti et al., 2015). Above ground, perennial ley can provide flowering resources throughout the cropping season, benefitting pollinators but also, through availability of diverse undisturbed habitats and available soil prey, strengthen arthropod predator communities (Scotti et al., 2015). In Sweden, leys are 7 to 10 times more common in organic than in conventional agriculture (Reumaux et al., 2023) illustrating their importance in systems that rely less on the input of agrochemicals. Including perennial leys into crop rotations and thus diversifying arthropod communities and their functions seems promising, but more research is needed on the legacy of growing perennial leys on arthropods, and in combination with other frequently applied practices of within field management.

Organic fertiliser

Inorganic fertiliser (i.e. mineral fertiliser) provides directly accessible nutrients to crops and thus increases plant yields (Tilman et al., 2002) but fails to support associated arthropod biodiversity in arable fields. In contrast, the diversification of nutrient supply to crops through organic fertiliser such as farmland manure or slurry can increase the abundance and diversity of beneficial insects above- and belowground (Aguilera et al., 2021; Viketoft et al., 2021). More specifically, the occasional addition of organic fertiliser can boost belowground decomposer communities as due to its ability to increase organic matter, water holding capacity, and soil structure creating favourable habitat conditions for many species (Francioli et al., 2016; Lin et al., 2019; Viketoft et al., 2021). Subsidisation of belowground communities with organic materials can, over longer times, increase yield through the slow release of nitrogen to the crop through species mediated soil processes reducing nitrogen leaching as seen for expensive inorganic fertiliser (Diacono & Montemurro, 2010). The benefits of habitat and food provision through organic fertilisation on belowground species have been shown to propagate into aboveground predator communities, where abundant and diverse predators increase pest regulation (Birkhofer et al., 2008; Riggi & Bommarco, 2019). Thus, organic fertiliser holds the potential to diversify communities in arable fields but its single and combined benefits with other practices are less well understood.

Tillage

Soil management practices such as tillage can affect soil quality through changes in the physical, chemical indicators with direct and indirect consequences for soil biodiversity (Lee et al., 2009; van Capelle et al., 2012). Tillage is widely applied in the EU as due to its ability to control pathogens and diseases and preparation of soils for the next crop (Hofgaard et al., 2016; Eurostat, 2017). Reducing tillage intensity or no till can benefit arthropod diversity (van Capelle et al., 2012; Müller et al., 2022), with remaining plant residues increasing habitat complexity, soil moisture and provide food and shelter for many taxa (Ayuke et al., 2019; Deleon et al., 2020). However, most tillage effects have been observed on small plots that are unlikely to support and retain communities of mobile species as they move well beyond the plot area (Jopp & Reuter, 2005; Boyce et al., 2017). We now need to study effects at the field scale with cross- season observations.

Within-field diversification practices have been identified to benefit crop production *via* strengthened biodiversity. My thesis assesses single and combined diversification and its impacts on several taxon groups above- and belowground, in open arable fields and across the crop-growing season. By that, I am generating new knowledge on how diversification of management practices align with species ecological habitat and resource requirements, ultimately determining their presence in crop fields.

1.2 Dynamic communities and their effect on ecosystem functions

There is consensus that biodiversity is essential for maintaining ecosystem functions (Loreau, 2000; Coleman & Whitman, 2005; Soliveres et al., 2016). In agroecosystems, many linkages between biodiversity and functions such as pest regulation, have been established in small plot or cage experiments constraining the biodiversity studied to a few selected species

(Macfadyen et al., 2009; Weisser et al., 2017; Aguilera et al., 2021). However, communities in open ecosystems are much more dynamic, with species moving in and out of the fields following available resources (Rand et al., 2006; Macfadyen et al., 2015). With such dynamic shifts in communities, biodiversity is changing across the crop growing season, and observations from manipulated experimental communities might not reflect the real importance of biodiversity across time. Effects must be explored at suitable spatial and temporal scales to understand the functions generated from biodiverse communities (Qiu & Cardinale, 2020). Because many functions are mediated within and across trophic levels, understanding the effects of diversity requires holistic assessments of within trophic, as well as across trophic complexity in response to management, and over entire crop growing seasons (Porazinska et al., 2003; Duffy et al., 2007).

1.2.1 Conservation biological control

Biological pest regulation is a key function in crop production to safeguard yields. The aim of conservation biological control is to reintegrate arthropod predators into cropping systems that feed on, and thereby regulate pests (Ehler, 1998; Begg et al., 2017). This strategy is based upon ongoing research that demonstrates a link between the conservation of arthropod predators and reduced pest pressures in arable fields. Protecting arthropod predator populations in agroecosystems has been shown to increase yields by 5-40% while decreasing pesticide use by 30-70% through relying on predators' pest suppressive effects (Pretty et al., 2018). However, herbivores can be an abundant but mostly ephemeral resource in agroecosystems. Therefore, predators need to be sustained on other “alternative prey” throughout time to unfold their pest suppressive effects at peak herbivore densities. In my thesis, I investigate the temporal dynamics of conservation biological control in open arable fields, with fluctuating communities of predators and prey.

1.2.2 Community assembly: within-field overwintering and its contribution to arthropod communities in arable fields

Assemblages in regularly disturbed arable fields are shaped by both predators immigrating into fields from surrounding habitats, but also species overwintering directly within the arable field (Holland & Reynolds, 2003; Macfadyen et al., 2015; Boetzl et al., 2022). Within-field management reduces predator communities' diversity and abundances, but how management shapes communities across season and through overwintering is less well understood (Holland & Reynolds, 2003; Hanson et al., 2017). The contribution of overwintering communities to overall predator assemblages in fields is seldom addressed (Djoudi et al., 2019), yet crucial to understand the across season legacies of management on predator communities and their functions in fields.

Disturbances in field, as created by soil tillage, can lead to the mechanical killing of overwintering life stages (Thorbek & Bilde, 2004; Shearin et al., 2007; Mesmin et al., 2020). These vulnerable life stages might also be more susceptible to reduced soil structural complexity and availability of organic material with intensified soil tillage (Bowers et al., 2021; Betancur-Corredor et al., 2022). Strengthening local overwintering and within-field community assembly can be especially important in simplified landscapes (Tamburini et al., 2016). Additionally, early within-field emergence after overwintering could lead to quicker establishment of predator communities within fields, and give communities a head start over later developing pest populations (Costamagna et al., 2015; Tortosa et al., 2022).

Therefore, management can have strong impacts of various community layers across time, and might affect the recovery of communities from disturbances.

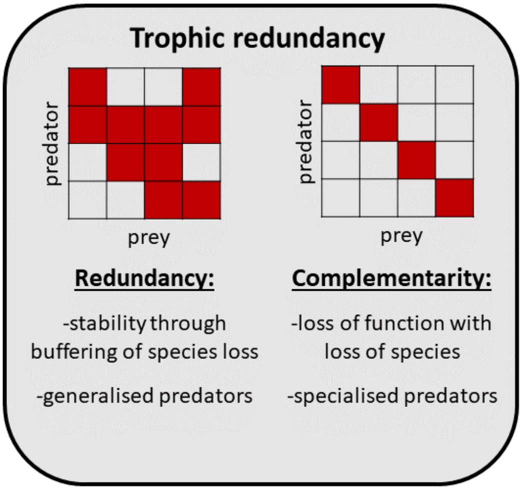
1.2.3 Alternative prey and its contribution to predator sustenance. Changes in predator-prey trophic interactions across crop growing seasons

Predatory arthropods such as carabids, staphylinids and spiders feed on herbivores and regulate their densities. Abundant and diverse communities of predators are efficient in regulating pests, especially when predator communities establish early in the crop season (Landis & Werf ,1997; Bowers et al., 2021). Early establishment, and sustenance of predator communities has been linked to the availability of soil prey. But effects have been studied in small cage or mesocosm experiments. In open arable fields, predators are presented with a much greater variety of prey items and their dietary preferences might be much more complex than in even experimental communities. Different prey choices such as feeding on soil fauna, intraguild prey could distract predators from consuming herbivorous prey.

Species interactions and their functions: trophic food webs

Ecological interactions among species drive communities and their ability to persist in a given environment. Across trophic level interactions connect within-trophic level biodiversity (i.e. predator diversity) with ecosystem functioning that is oftentimes generated across trophic levels (Duffy et al., 2007). For example, species interactions across trophic levels shape the delivery of biological pest regulation through predators feeding on (pest) prey. Such interactions can be represented in food webs with species represented as individual nodes that, through interactions, are embedded in a wider network of species within a community. Such ecological networks describe the properties of nodes (or species) but also the emergent properties of the entire network on the structure of the community (Heleno et al., 2014). This is especially useful for assessing the biodiversity-functioning relationship as networks encompass two key properties: diversity in the trophic levels and biomass flow between trophic levels, linking the biodiversity to interaction structures and functions. An emerging area of mainly theoretical research has begun to explore how food web structure (i.e. which species interact with each other) drives the delivery and stability of ecosystem functions (Thébault & Loreau, 2006; Poisot et al., 2013; Schneider et al., 2016). However, the accuracy of insights gained from analysing interaction networks is limited by the quality of data used to infer interactions in complex natural communities.

As an example, assume a node in a network represents a single prey species. The number of links to that node will define the preys’ vulnerability to predation (Bersier et al., 2002). When numerous nodes at different trophic levels are considered, the structure of interactions between these nodes represent the trophic interaction structure of the communities. When several higher trophic level species (i.e. predator) share links to the same prey, their resource use is “redundant”. If predators share very little or no common prey, their resource use is “complementary” (Box 1). The outcome of functions shaped by such interactions, can vary depending on where communities are located along the resource-structure gradient.



Redundancy:

-stability through buffering of species loss

-generalised predators

Complementarity:

-loss of function with loss of species

-specialised predators

Box 1. Conceptualisation of trophic interaction structures in predator-prey networks with either trophic redundancy (i.e. predators sharing the same or similar prey items) or complementarity (i.e. predators differ in their resource use).

Redundancy in resource use can help to stabilize functions by ensuring them against species loss (Peralta et al., 2014; Feit et al., 2019). This is most common in generalist ecosystems when predators' trophic preferences overlap and functions can be taken over by other species in the community. Complementarity in resource usage, on the other hand, can improve functioning by boosting the efficiency of interactions between trophic levels. In predator-prey interactions, specialisation on resources can reduce search, handling, and ingestion time (Wootton et al., 2023; Dainese et al., 2017). However, such complementarity leaves the system more vulnerable to functions being lost with the loss of individual species generating them.

In agroecosystems, this becomes relevant when we aim to understand how the configuration of communities and the structuring of predator-prey interactions promote or weaken the delivery of ecosystem services, such as biological pest regulation, which is a direct result of predator-prey trophic interactions. The quality of data in assessing the explicit links between predator and prey, however, limits the insights into functioning gained through analysing interaction networks. The use of structurally explicit food webs to anticipate ecosystem performance has been consistently advocated for, but has yet to be fully realized (Duffy et al., 2007; Cardinale et al., 2012). This has been at least partly due to methodological limitations in acquiring high-resolution data, which only have recently become available with advances in molecular sequencing techniques. Open environments, such as arable fields, can have complex networks due to the abundance of potential prey from both above- and belowground, requiring high resolution of data on who eats whom.

While current molecular advances aid to unravel the linkages between dynamic prey communities and predators' prey choice in open fields, studies assessing both the availability of prey and the realised trophic interactions are rare, especially across agricultural management practices (Roubinet et al., 2017). While predator gut content screening for target prey reveals complementary prey choice by predators and functional redundancy across the crop growing season (Roubinet et al., 2018), these approaches might neglect other important trophic interactions sustaining predators in open fields that are not included as target prey in analysis. Further, selecting only a few target prey reduces the structural complexity of food webs, making it impossible to link structures to functioning.

We now need to empirically tackle the relation between food webs and functions, especially for those that operate across the above- and below-ground interface and across time (Ramirez et al., 2018). Arthropod predators can have strong dietary preferences (Saqib et al., 2021) but might depend on the availability of different prey throughout time (Östman et al., 2003; Birkhofer et al., 2011). Differences in feeding behaviours across species or time can affect predator communities' effectiveness and resilience to perform biological pest regulation. To address these knowledge gaps, within this thesis, I map out how trophic interactions vary over the cropping season, to determine whether management provides all of the required resources.

While agroecosystems have to be addressed as a whole, many of the desired functions are provided by local communities in the soil or dwelling in the crop fields. This highlights the need to address species ecology and the mechanistic links between management, biodiversity and ecosystem functioning at the field scale. **In this thesis, I am extending our knowledge on the functioning of agroecosystems by assessing changes in communities across management practices, throughout and across the crop growing seasons. Thus, I will further elucidate the mechanistic linkages between biodiversity and ecosystem functioning**.

2. Aims

The overarching aim of my thesis is to improve our understanding of the **effect of agricultural diversification** on **soil fauna**, aboveground **arthropod predators** and **their interactions** across the above- and belowground interface and over time.

- Explore how diversification through organic amendments and extended crop rotations with perennial leys (**paper I**) or tillage intensity (**paper II)** affect communities above- and belowground and their trophic linkages (**paper III**).
- Investigate the role of complementary resources, i.e. herbivores and soil fauna in aboveground arthropod predators' diet (**paper I& III**), and explore the consequences for the structure of predator-prey-food webs and ecosystem functioning with management-induced changes of the availability and diversity of resources (**paper III**).
- Assess above- and belowground communities ability to recover from agricultural disturbance (**paper II**).
- Quantify the effect of disturbance from tillage on local community assembly by confronting within-field overwintered arthropods with circulating ground dwelling arthropod predators (**paper IV**).

In doing so, I aim to contribute to our understanding of management impacts on the ecology of associated biodiversity to the agroecosystem.

3. Methods

To address the overarching aims of my thesis, I collected data on community composition of above- and belowground communities (**paper I and II**) as well as trophic interactions (**paper III**) and overwintering of predator communities within arable fields (**paper IV**). With these data, I was able to describe changes in arthropod communities, resulting from agricultural management practices. Further, using these datasets in different combinations (Figure 3) allowed me to address the underlying mechanisms of community assembly both, within the crop growing season by studying predator prey trophic dependencies across time and availability of prey (**paper III**), and between crop growing seasons, assessing the direct effect of management on the local community assembly *via* within-field overwintering and comparing communities before and after management (**paper II** and **IV**).

3.1 Study sites and regions

All papers presented within this thesis are based on data collected in two field experiments with different diversification managements but similar ecological questions about community assembly, structuring and interactions across the above- belowground interface. In the following, I will explain the experimental set-up and specific study questions associated with each field experiment. For detailed protocols, see individual chapters.

3.1.1 Single and combined diversification: organic fertiliser and perennial ley

To assess the effect of single and combined diversification on communities and their interactions across the above-, belowground interface, I collected data in 2020 in Halland County (N56.895, W 12.631). I collected data three times during the crop growing season at tillering, heading and ripening of the crop on 19 conventionally managed arable fields to track changes in communities across the growing season. Fields were selected based on their management history in, at least, the past five years to study the legacy of agricultural management on assemblages of species communities. The fields were selected according to three contrasting management practices: annual crop rotations with mineral, or organic fertiliser and fields with perennials in the crop rotation in combination with organic fertiliser. To observe the legacy effect of perennials in the rotation, rather than immediate pre crop effects, fields were selected so that there were no perennials in the two years prior to our study (Figure 1).

In **paper I**, I sampled for above- and belowground communities (see section 3.2.1) to ask how management history affected coupled communities of soil fauna, herbivores, weeds and predators. This data was complemented by mapping out explicit links between predators and their available prey (**paper III**) using molecular gut content analysis (section 3.2.2). In both papers, I assessed changes in communities and the availability of prey across the crop growing season to identify potential resource discontinuities with changes in agricultural management.

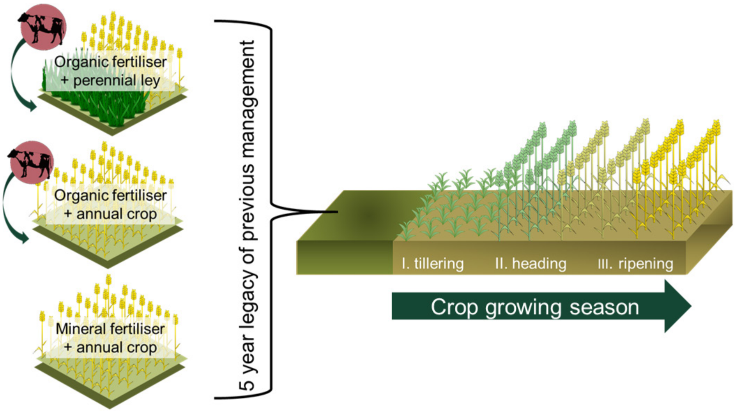


Figure 1. Experimental set-up and treatments for assessing the single and combined effects of organic fertiliser with or without perennial leys in the crop rotation on arthropod communities in spring cereals. Illustration: Janina Heinen.

3.1.2 Management intensities: tillage

To investigate the effect of tillage intensity on communities above- and belowground as well as community assembly across years, I used data collected in Västra- Götaland County (N 58.433 W13.011) in 2020 and 2021. Data was collected on 30 fields with varying tillage intensities ranging from high intensity inversion tillage, and reduced tillage to no till practices. Treatments were chosen to reflect intensity of disturbances of habitats and its effects on communities above- and belowground as well as their ability to recover from disturbance. Fields were sampled before tillage management, after tillage was implemented between crop changes in autumn 2020, and throughout the crop growing season in 2021 (Figure 2). Fields were initially sown in winter cereals and after harvest, all fields were sown in winter oilseed rape (WOSR). I described communities before and after tillage both above- and belowground (**paper II**) to assess changes in the density and richness of communities (see section 3.2.1) with varying tillage intensities. I especially focussed on the recovery of communities and the temporal linkages between belowground prey and aboveground predators. To mechanistically test the effect of tillage on community assembly in fields I measured the overwintering of predator communities in arable soils across the three disturbance intensities (**paper IV**, see section 3.2.3). This dataset gave me the possibility to compare resident and circulating communities in arable fields to determine the effect of local disturbances on arthropod communities through tillage.

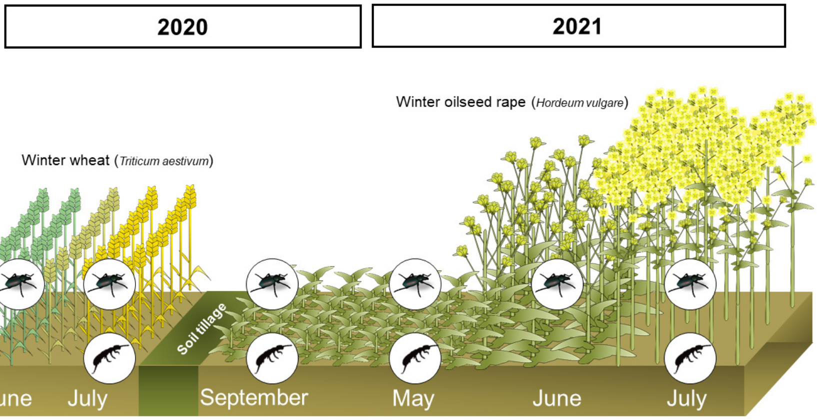


Figure 2. Experimental set up including the sampling rounds for aboveground predators (round icons with carabid symbol) and soil fauna (round icons with collembola symbol)

in 2020 and 2021. Fields were sown in winter cereals before soil tillage in August 2020. After tillage all farmers sowed winter oilseed rape in late summer 2020. Aboveground predator communities were sampled at each sampling round. Soil mesofauna communities were sampled only in July and September 2020 and May and July 2021 (paper II). Illustration: Janina Heinen.

3.2 Data collection and processing

A wide array of data was collected and used in various combinations in **papers I-IV** (Figure 3). The aim was to describe communities' responses to agricultural management and complement this knowledge with in-depth assessment of mechanistic links between management and species ecology.

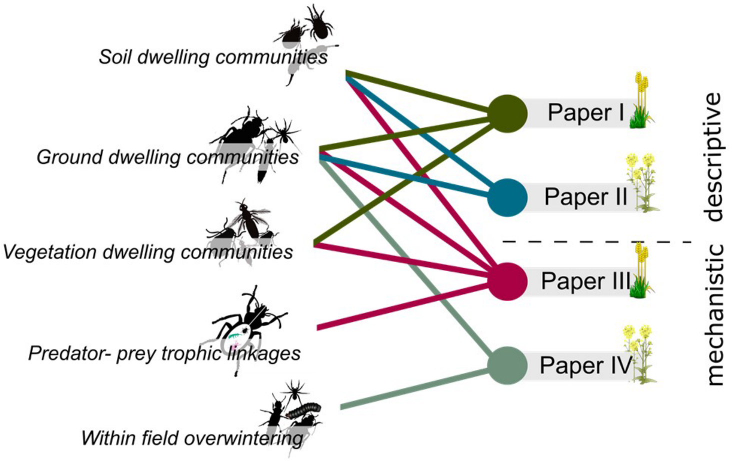


Figure 3. Overview of how the data on community composition, trophic interactions and within field overwintering were used in **paper I-IV**. Paper I and II used community data to describe the occurrence and abundances of species above- and belowground as a results of management, whereas paper III and IV focussed on the mechanistic linkages between management induced changes and the resulting consequences for trophic interactions (paper III) and community assembly in arable fields (paper IV). Icons of either cereal crops in combination with ley grasses or oilseed rape crops indicate that paper I&III were based off data collected in Halland, 2020, whereas paper II&IV used data collected in Västra Götaland, 2020-21. Illustration: Janina Heinen.

3.2.1 Community densities of predator and prey

Assessment of soil dwelling communities

I sampled for soil mesofauna, as they perform important ecological functions in the soil food web, enhancing the capacity to decompose organic materials and release nutrients to crops, but secondly can constitute alternative prey to predators. I extracted soil core samples (5 cm diameter, 10 cm depth) using Tullgren funnels (Figure 4, Tullgren, 1918). Soil mesofauna were categorised into coarse groups of collembolans, mesostigmatid mites, oribatid mites, juvenile mites and other arthropods (<2 mm e.g. millipeds). I calculated their densities as the number of individuals per soil corer. These data were used to assess the effect of agricultural management practices on soil mesofauna communities (**paper I&II**) and the availability of soil fauna as alternative prey to predators (**paper III**).

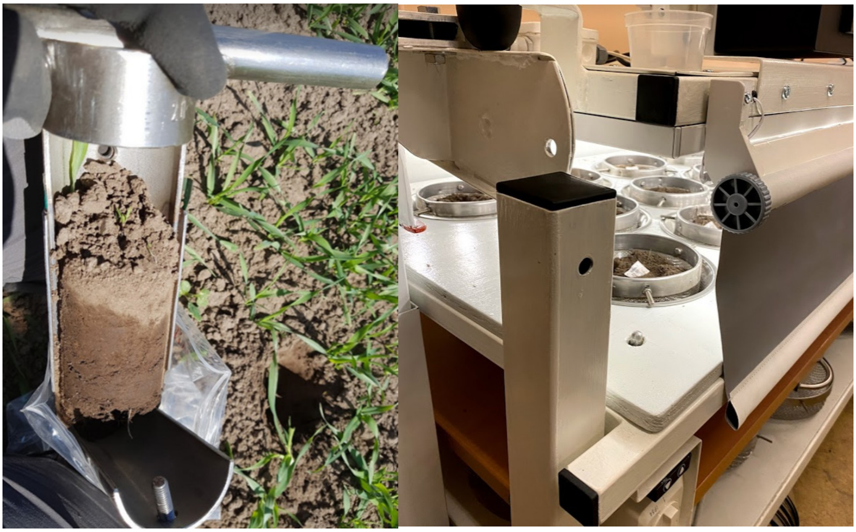


Figure 4. Intact soil core sample taken to a depth of 10 cm in barley fields (left) and extraction of soil mesofauna using Tullgren extraction in the laboratory (right). Photo: Janina Heinen.

Assessment of ground dwelling communities

Ground dwelling arthropod predators such as carabid and staphylinid beetles as well as spiders are important biological pest regulation agents. Therefore

I assessed the density and diversity of predator communities in fields and across agricultural management. I captured their activity density using wet pitfall traps (**paper I, II, III, IV**). These data were used to describe community composition in response to management but also to estimate the availability of intraguild prey i.e. predators consuming other predators. Pitfall traps consisted out of a plastic cup (10 cm diameter, 12 cm height) sunk flush with the surface of the ground, filled with water into which invertebrates inadvertently fall (Figure 5; right). All captured individuals belonging to carabids and spiders were identified to species and all staphlylinids to genera. Densities were assessed as the number of individuals per sample and taxonomic richness as the number of species or genera per sample. Using this technique allowed me to compare activity densities over time and across treatments. These data were used in all papers to either describe changes in communities or complement them with additional data on mechanistic links between predators and their prey (**paper III**) or communities colonising fields *versus* local assembly (**paper IV**).

Assessment of vegetation dwelling communities

Many crops are attacked by herbivores located in the crop canopy. I used sweep netting (**paper I & III**) to assess the abundance and taxonomic richness of vegetation dwelling invertebrates to estimate the availability of prey to predators and the potential herbivore community density to be regulated by predators. This method involves passing the net through the crop using alternating strokes from left to right. I sampled communities of vegetation dwelling invertebrates twice during the season when crop height allowed sampling with this technique. Caught invertebrates were identified to genera. I calculated the abundance of herbivores caught with this technique as the individuals per sample and their taxonomic richness as genera per sample. These data were used to measure their availability as prey to predators (**paper I**) and specifically, were incorporated in the assessment of herbivore regulation through trophic interactions of predators and prey (**paper III**).

3.2.2 Predator- prey interactions

To characterise trophic links between species (i.e. who eats whom), I drew on molecular-based gut content analysis. Since the amounts of DNA analysed are oftentimes minute, a common challenge is that specimens collected in different types of mass samples (wet pitfalls, sweep nets etc.) will easily contaminate each other with DNA through the collection medium. Thus, I needed to collect samples within which the specimens were in little contact with each other, and to handle the samples with specific focus on avoiding cross-contamination with DNA residues.

Specimen collection for DNA metabarcoding

To obtain uncontaminated samples, I set out dry pitfalls to collect specimens (Figure 5; left, **paper III**). Pitfalls were operated at three times during the season (tillering, heading and ripening of the crop) to capture changes in predator diets over time. Dry pitfall traps consisted out of a plastic cup (10 cm diameter, 12 cm height) dug flush with the soil surface, filled with wood chips to catch live carabid predators. I added wood chips for carabids to hide and thus to circumvent predation in the pitfall traps. Pitfalls were operated for 24 h to avoid degradation of DNA in predators' guts, and collected specimen were transferred head first into Eppendorf tubes until regurgitation in the laboratory.

In analysing prey DNA in samples of predatory arthropods, a common issue is that the DNA of the predator will oftentimes swamp any signal from the prey. Thus, I aimed to maximize the ratio of prey-to-predator DNA by using predator regurgitates. Carabid predators within tubes were therefore dipped into a cup with hot water to provoke carabid regurgitation. Regurgitate was then resolved in buffer and frozen at -20ºC until molecular analysis. Live carabids were released into their natural habitat after the experiment.

Figure 5. Dry (left) and wet (right) pitfall for catching carabids. Photo: Janina Heinen

Molecular characterisation of trophic interactions

Characterisation of trophic linkages between carabid predators and their prey was based on DNA metabarcoding. I chose DNA metabarcoding as species are tied into a multitude of ecological interactions, especially in open fields. Metabarcoding can, as opposed to other molecular and observational methods, depict multiple prey items at the same time without requiring a pre-selection of target prey items (Rennstam-Rubbmark et al., 2019).

A detailed description on the molecular methods are given in **paper III**, but in short, using direct incubation of the samples that were then purified using magnetic SPRI beads, I extracted DNA from regurgitate samples (Vesterinen et al., 2016). Following extraction, DNA was amplified using the primers fwhF2+fwhR2n, which targeted the DNA barcode region of the arthropod mitochondrial cytochrome oxidase subunit I (COI) gene region (Vamos et al., 2017). The NGS-library preparation followed Vesterinen et al., 2018. Sequencing was performed through an Illumina NovaSeq6000 SP Flowcell v1.5 PE 2x150 run (Illumina Inc., San Diego, California, USA). The reads obtained from sequencing were merged, trimmed for primers, dereplicated into unique haplotypes, denoised into sequence variants (ZOTUs), assigned to taxa, and finally mapped to a zotutable.

Predator- prey networks and herbivore regulation

Based on links revealed through molecular sequencing of gut contents, I constructed predator-prey networks as a matrix between predators and their prey. Trophic networks provide the possibility to study multiple interactions at the same time and describe interactions though the structure of links between species. Through that, we can analyse interactions beyond the simple descriptions of who ate whom but determine which predators share prey, which prey is preferably eaten and which structural linkages shape the predation of target species i.e. herbivore regulation. Predators were added at a species level whereas prey was added at the genera level as to high confidence in taxonomic assignment of DNA sequences at this level. I separately analysed the structure of predator-prey networks for herbivorous, soil mesofauna and intraguild prey.

Based on the constructed networks, I calculated the “vulnerability of prey” as the average number of predators per prey item in the network, summed across all observed trophic links (Williams & Martinez, 2000; Bersier et al., 2002). Secondly, I calculated “predators’ trophic redundancy” as the mean number of shared partners as a matrix of the number of prey species shared by each predator species (Roberts & Stone, 1990; Stone & Roberts, 1992). Details on calculations and justification of metric choices can be found in full detail in **paper III**.

These data were used to assess dietary changes in communities with changing community composition as a result of diversification management and changes of communities' diet preferences across time in the crop growing season. This dataset allows us to study predator sustenance and herbivore regulation across management practices in open arable fields.

3.2.3 Predator overwintering

Community assemblages sampled with pitfalls confound species overwintering in the arable fields and species immigrating into fields from surrounding habitats. In order to form a mechanistic understanding of how management affects predator community assemblages in fields and across growing seasons, I assessed the within-field emergence of predators across different tillage intensities. To that aim, I set out six emergence traps per field covering a total of 0.57 m^2, in a total of 29 fields. I operated emergence traps throughout the cropping season from early March until harvest of WOSR in July. Emergence traps consisted out of a metal barrier dug 10 cm deep into the soil, closed and secured with a fine mesh to avoid emigration and immigration. Emerging predators were caught using a pitfall trap inside the barrier (Figure 6, right).

Figure 6. Emergence trap set-up with 2 sets of emergence traps dug 10 cm into the soil and closed with a fine mesh secured with a belt to avoid emigration and immigration of insects in and from the emergence trap (left). Top view into the emergence trap with a pitfall dug flush with the soils surface to catch emerging predators. Photo: Janina Heinen

4. Results and discussion

I present evidence that diversifying agricultural practices through soil amendments and lowered soil disturbance (either through perennial ley or reduced tillage intensity), builds abundant and species rich communities of arthropods in arable fields. I show that the legacy of combined diversification with organic fertiliser and ley creates abundant and diverse communities above- and belowground (**paper I**), and that such diverse predator communities result in increased pest regulation (**paper III**). Within that frame, I show that in open field experiments, diversification leads to early available soil prey which can sustain predators in arable fields, and that the predators' diets are complemented by the consumption of herbivorous and intra-guild prey throughout the cropping season (**paper III**).

With high intensity of tillage management, the densities in both above- and belowground communities are reduced (**paper II**). Effects are short lasting with soil fauna and most aboveground arthropod predators (except spiders) recovering in spring following late summer tillage. Persistent effects on spider communities throughout the crop year highlight that management can affect taxon groups differently depending on their varying habitat needs (**paper II**). Tillage intensity only marginally affects overwintering communities, with enhanced density of overwintering individuals under inversion tillage but higher diversity of predator communities in the untilled fields. Nonetheless, I show that emerging communities are distinct from predator communities caught in open fields in early season and that within field overwintering is important for community assembly in arable fields (**paper IV**).

4.1 Consistent imprint of diversified management on belowground soil mesofauna due to increased soil habitat quality

I find that diversification of agricultural practices increases the density of soil mesofauna. Increased densities are likely attributed to improved belowground habitat quality and availability of resources to soil mesofauna. Under reduced tillage intensity, more plant residues remained on the soil surface (**paper II & IV**), which increased soil moisture in these fields (Figure 7). Similarly, the combined diversification with organic amendments and perennial leys increased the amount of soil organic matter in fields, thus increased the water retention capacity, which resulted in higher soil moisture than in the non-diversified fields (**paper I**).

Soil moisture is a crucial habitat requirement for all soil dwelling arthropods as it prevents soft-bodied species from desiccation (Tsiafouli et al., 2005). Additionally, remaining plant residues with no till or reduced tillage can provide shelter from predation and increased SOM can provide food resources for soil fauna (Lin et al., 2019). Together, **management diversification provides favourable conditions for associated belowground communities** (Crotty et al., 2016; Emmerling et al., 2021; Hoeffner et al., 2021). Soil arthropods are involved in important processes such as nutrient cycling and decomposition. Such processes release nutrients to crops and support sustainable cropping systems by replacing the need for mineral fertiliser (Diacono & Montemurro, 2010). With complementary soil analysis (**paper I**) I show that the nitrogen, carbon and SOM contents of soils increase under diversified management, but this was only found for the combination of organic fertiliser and perennial ley (Figure 6, paper I). **My results show that combining management practices can have greater benefits than single practices, where effects might be more dependent on initial conditions in the field** or in the case of paper I, the different types of organic fertilisers used (Viketoft et al., 2021; Heinen et al., 2023).

Both the inclusion of perennial leys but also reduced or no till disturbance increases habitat continuity for soil mesofauna. Especially repeated disturbance can impair communities' functioning, as some species will not be able to sustain disturbances and recolonise fields. I did not have the capacity to identify soil mesofauna to species level, but such analysis could further show how management affects communities within instead of only across taxa. I show a strong imprint of perennial leys that were in the fields for three years, and its long lasting legacies. This, shows that **providing habitat continuity across and between the crop growing season will foster abundant soil mesofauna communities**. The disturbance under inversion tillage consistently decreased soil mesofauna abundances across all taxon groups, suggesting that severe destruction of habitats is detrimental for all individuals in the community. Increased soil fauna densities under reduced tillage however, show that intermediate disturbance might benefit some individuals in the community. If these results stem from a single species, being greatly enhanced under disturbance or general benefits of intermediate disturbance on all species is not to be addressed on coarse taxon resolution data. Overall, **my results show that suitable habitat conditions for soil fauna, translate into enhanced soil mesofauna densities in crop fields** (Figure 7).

Although not presented in this thesis, I sampled for bacteria and fungi communities, in field experiments looking at the effect of organic fertiliser and perennial ley conducted in Halland 2020. Additionally, I brought out decomposition bags and nutrient resin strips to assess functions under differing management. These data remain to be analysed but could further elucidate the link between management, entire food webs across more trophic levels, and the nutrient availability to crops. Bacteria and fungi communities are tightly linked to the release, and the cycling of nutrients. Studying a more encompassing soil food web across trophic levels of meso- and micro- fauna would help in understanding how management shapes belowground processes and functions (Lavelle et al., 2006).

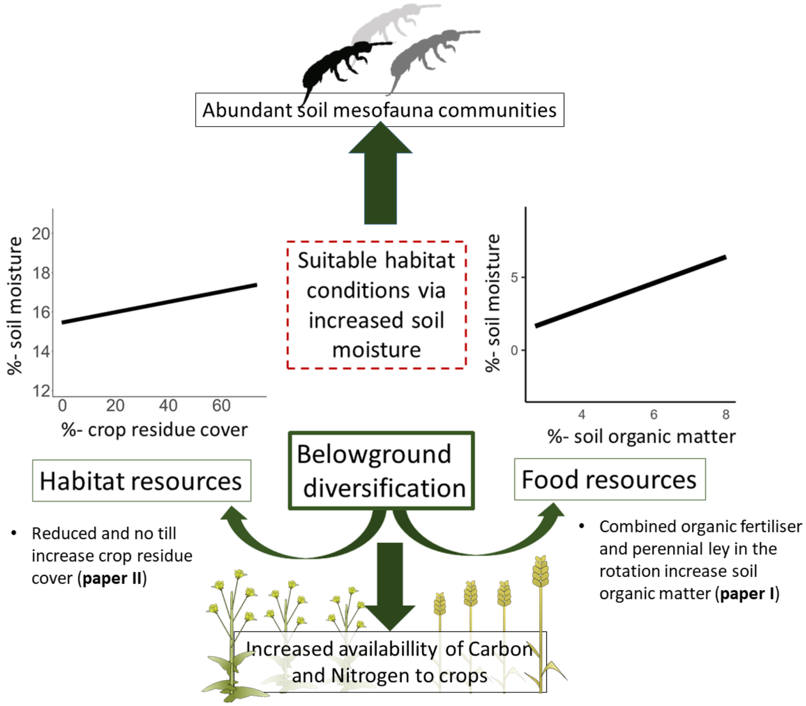


Figure 7. Belowground diversification effects on the availability of carbon and nitrogen to crops as well as diversifications' potential to provide habitat resources in form of remaining crop residue after soil tillage, and food resources in form of soil organic matter under combined diversification with organic fertiliser and perennial leys in the rotation. Both, the amount of crop residue, and soil organic matter show the capacity to increase soil moisture, which creates suitable habitat conditions for, and fosters abundant soil mesofauna communities (**paper I** and **II**). Illustration: Janina Heinen.

Further, I show that **increased density of soil mesofauna in some cases (paper I) coincides with greater density and diversity in aboveground predator communities**. This suggests that increasing food resources (soil fauna) to predators from the belowground communities could have bottom-up effects on predators, potentially increasing top-down regulation of herbivores (see **paper III**). Specific trophic linkages between soil mesofauna and predators are discussed in section 4.3 below.

4.2 Within-field emergence aids community assembly but timing of management likely shapes across season legacies on communities

Not only soil mesofauna depend on suitable soil habitats. Soil dwelling life stages of arthropod predators are in the same need for habitat complexity and available resources while overwintering in arable soils and can thus be affected by management, especially soil tillage. Strengthening within-field overwintering can be important to build abundant and diverse communities of predators (Hanson et al., 2017; Hoeffner et al., 2021; Boetzl et al., 2022).

I find that **fields are important overwintering habitats with hundreds of individuals emerging per m^2 of arable soil** (Figure 8, **paper IV**). High densities of predators overwintering within fields can become important for pest regulation. Although, many studies suggest that early present predator communities will supress abundant pest species in the beginning of the crop growing season (Zaller et al., 2009; Costamagna et al., 2015), I find potentially interacting effects of management with pest and predator emergence. While I find lower pest emergence in no till fields compared to reduced and inversion tilled fields (**paper IV**), I find increased densities and diversity of predators in autumn the year before emergence (**paper II**). I suggest that abundant and diverse predator communities late in the season can supress pest species overwintering by regulating the adult pests at the time of oviposition in fields. Thus, effects of before overwintering suppression of pests might be beneficial for the regulation of crop pests by adding to predators controlling pest densities during the crop growing season.

I found overwintering predator communities to be similar across tillage intensities with marginally higher diversity under no till and increased overwintering densities under inversion tillage. I suggest that timing of soil tillage operations and the management associated to the crops grown strongly determines if predator communities are affected (Boetzl et al., 2022). Tillage operations that are within the activity period of predators, thus giving them the opportunity to avoid disturbance and recolonise fields later on, seem less detrimental for many overwintering communities (Holland & Reynolds, 2003; Sutter et al., 2018). That being said, the increased diversity of predator communities overwintering illustrates that reduced tillage management can create habitats that sustain a greater variety of species, potentially building diverse communities over time. But, many predators are well adapted to agricultural disturbance, which leads to homogenisation of communities though filtering for the species that can actually be sustained despite disturbances (Lichtenberg et al., 2017). I also find that **in the overwintering communities, a large core group of species is shared among all tillage intensities**, hinting at longer term legacies with homogenisation of predator communities under repeated disturbance in arable fields. Greater overwintering densities in inversion tillage fields might be attributed to some species coping well with disturbance (Holland and Reynolds, 2003) or, species recolonising field after inversion tillage due to exposed soil prey and fungi on the soil surface potentially providing accessible prey to predators.

I find that overwintering and circulating ground dwelling communities are distinct early in the season but homogenise as the crop growing season progresses. This again shows that within-field overwintering can aid to build predator communities within fields. The homogenisation over time is potentially the result of species moving in between the landscape and the fields (Rand et al., 2006). Adapting management practices to provide year round suitable within-field habitats that can sustain predators throughout their entire life cycle can reduce the dependency of colonisation of fields from surrounding habitat. This is especially important in simplified landscapes that cannot provide sufficient colonisation fields by communities in other habitats entering the fields (Öberg et al., 2008; Tamburini et al., 2016).

I suggest that reduced management in general, but importantly in alignment with arthropods life history traits, can diversify communities in fields. Lowered intensity of tillage benefits soil fauna, soil dwelling predator life-stages and thus can have long term benefits of diverse aboveground adult predator communities and their ability to regulate pests.

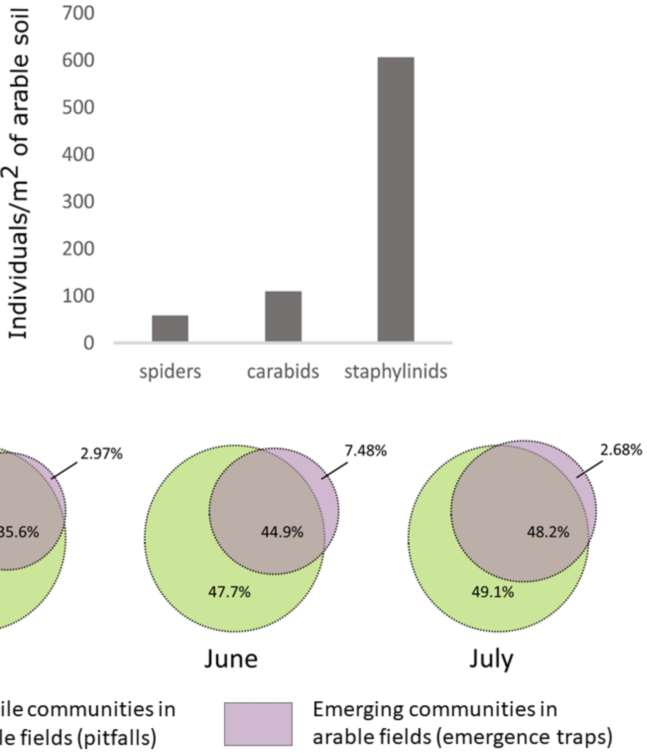


Figure 8. Cumulative number of individuals emerging across the crop growing season, split by the three predator groups: spiders, carabids and staphylinids per m^2 of arable soil, averaged across fields. Venn diagrams show the overlap of mobile communities (pitfalls, green), the emerging communities (purple), and the percentage of species found uniquely in either of the sampled communities in May, June and July (adapted from **paper IV**).

4.3 Habitat and resource continuity: above and belowground dynamic communities under contrasting management

While the timing of management can be important in sustaining communities across time, it also impacts linkages between species, potentially leading to temporal mismatches of densities and dependencies, and creating potential resource bottle necks across the season.

4.3.1 Similar effects of diversification on above- and belowground communities

I found that **diversification aids coupled above- and belowground communities, as seen in similar responses of diversification on soil mesofauna and aboveground arthropod predators** (paper I and II). The diversification practices investigated in this thesis differed on the temporal scales they operated on. While reduced tillage intensity had strong immediate effects on species communities *via* habitat and resource continuity with remaining plant residues (**paper II**), we observed legacy effects of reduced disturbance through perennial ley and the provided habitat continuity for communities over time (**paper I**). I found a clear imprint of diversification with perennial leys on communities above- and belowground. I conclude that the legacy of lowered disturbance through ley persisted for several years after the transitioning from perennially to cereal crops (Lemaire et al., 2015). Perennial leys can increase habitat complexity for several taxa through altered soil structure and differences in root structures compared to annual crops and increased SOM (Hernanz et al., 2009; Marshall et al., 2016). The highest abundances of predators taken together were found in fields of combined diversification. This suggests that predators potentially benefit from using complementary resources, and their abundance increases further when other prey, such as herbivores, become available later in the cropping season. This assumption was tested by assessing specific linkages between predators and complementary prey in b of this thesis and is discussed in detail below.

4.3.2 Complementary food resources sustain predator communities: trophic interactions across time

Arthropod predators, such as carabids examined in this thesis, are feeding on a variety of resources. My thesis shows that **soil fauna, herbivores, and intra-guild prey are important food resources to predators, complementing each other across the crop growing season** (paper III, Figure 9A). I find that soil fauna is an important part of the predators' diet during early cropping season but becomes less vulnerable to predation over time, whereas herbivores gain importance in the predators' diet as the crop growing season progresses. The vulnerability of intraguild predation was high across the whole crop growing season. Intraguild predation is widespread around generalist arthropod communities (Rosenheim &

Harmon, 2006). Intraguild predation can mediate the co-existence of predators in fields as it allows individuals to meet their nutritional requirements when other prey is scarce, while simultaneously lowering competitor densities (Holt & Polis, 1997; Uiterwaal et al., 2023). Recent gut content analysis in open cropping systems found high intraguild predation in spiders that in combination with other sporadic food resources shaped the diet composition of predators (Saqib et al., 2021). Intraguild predation can however, distract predators from consuming target prey at peak pest densities, which is why the combined assessment of various food resources is highly valuable.

I find that depending on the management in fields, the vulnerability of the three prey groups studied (herbivore, soil fauna, intraguild prey) display varying trajectories in time (Figure 9B). Under combined diversification with organic fertiliser and perennial ley in the crop rotation, soil fauna were highly available prey to predators (**paper I**) and were also preyed upon frequently by predators early in the season (**paper III**). The dependency on both soil fauna and intraguild prey was reduced over time in the diversified fields where as it increased or remained stable under mineral fertilisation or organic fertilisation with annual crops. **I suggest that, diversifying practices supports species rich predator communities that can increase biological pest regulation, as due to their decreased interference of complementary food resources with the consumption of herbivores over time.** Additionally, herbivore vulnerability was stable in diversified fields whereas it increased over time to the level of that of the diversified fields. Early on established predator communities in fields can give communities a head start over later developing pest population and increase the overall crop protection over time (Landis & Werf, 1997; Costamagna et al., 2015). Therefore, the continuous supply of available prey to predators can have implications on their ability to control pests at peak pest densities.

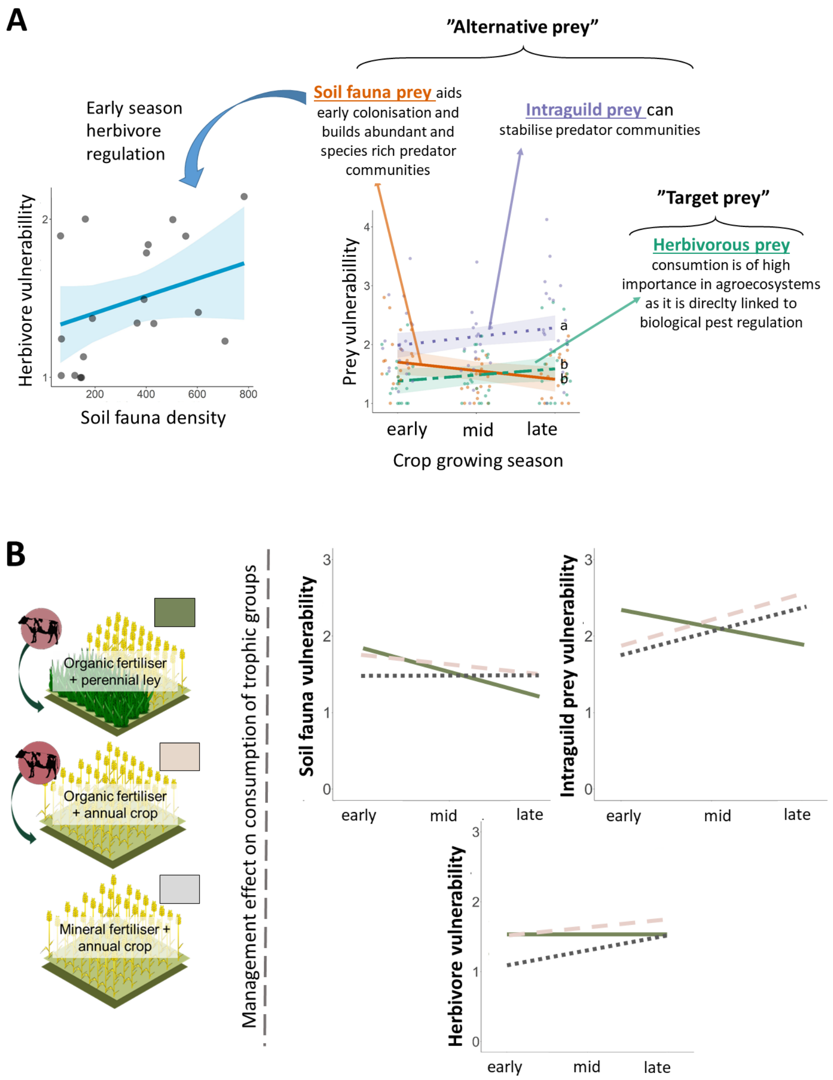


Figure 9. The role of complementary prey across the crop growing season and under diversification with organic fertiliser with or without perennial ley in the crop rotation. Figure is adapted based on results found in **paper III**. Illustration: Janina Heinen.

I show that communities above- and belowground are linked through trophic interactions, especially across time. I contribute new knowledge on predators resource use in open fields, and across entire crop growing seasons. Predator communities diet preferences changing over time underlines the importance of studying dynamic communities and their interaction as opposed to snap shot assessments at peak herbivore densities. I extend on studies performed in mesocosms or cage experiments and confirm, at the field scale, the key assumption that soil fauna is important prey to predators over time (Birkhofer et al., 2008; Roubinet et al., 2017; Aguilera et al., 2021). Importantly, I do so in dynamic and uneven communities of predators (Winfree et al., 2018), and show that complementary resource use is a key to build abundant and species rich communities, especially under diversified management, where many complementary resources in combination with favourable habitat conditions translate to enhanced pest regulation (Roubinet et al., 2018). The insights gained from explicit linkages between predator and their prey can inform its impacts on pest regulation (4.4).

4.4 Strong imprint of predator diversity and redundancy on herbivore regulation

Drawing on molecular gut content analysis, **I identified predators' trophic redundancy (i.e. predators feeding on similar prey) to be the structuring property among predators, and herbivore regulation to increase with increasing trophic redundancy and predator species richness** (paper III, Figure 10).

Generalist predators have been shown to be highly redundant in their resource use (Wirta et al., 2015), which can insure the stability of functional responses even when selected predator species are lost (Feit et al., 2019). With this thesis, I extend on the current knowledge on predators feeding interactions by mapping out explicit links, at high taxonomic resolution, between predators and prey in open fields and across time. Metabarcoding of predator gut contents allowed me to identify eaten prey on a high taxonomic level and thus, generate structurally complex food webs. Such well-resolved food webs have repeatedly ben called for and, by processing large quantities of samples, I contribute important knowledge with these well resolved food webs across time (**paper III**). Understanding the structural complexity and the resulting generation of ecosystem functions becomes highly relevant in constantly disturbed agroecosystems where services, such as pest regulation, have been recognised to be enhanced with diverse predator communities. More diverse predator communities exploit a greater variety of resources (Byrnes et al., 2014), and biodiversity associated to agroecosystems can aid ecosystem functioning, such as biological weed and pest control (Soliveres et al., 2016), allowing the coexistence of abundant service-providing aboveground predator communities. My thesis contributes to our knowledge on biodiversity ecosystem function relationships in arable fields by extending on our current knowledge that is largely based on target prey screening of predators guts (Roubinet et al., 2018). I was able to map out larger food webs and unravel the structural complexity of interactions arising from changes in the diversity in the higher trophic level (i.e. predators) with treatment manipulation of assembled communities in open fields. Specifically, the linkages and predators' prey choice to a variety of herbivorous prey as opposed screening for a single target prey are important to reveal, thus structural complexity in interactions across several herbivore prey. **Further, I showed that the best determinants of herbivore control were largely linked to trophic structures and within trophic level complexity, and to a much lesser extent on the density and diversity of communities sampled independently in fields. This underlines that we need to understand the emerging structures in food webs based on the changes management imposes on arthropod communities in fields, especially as the linkages between above- and belowground communities are strong.**

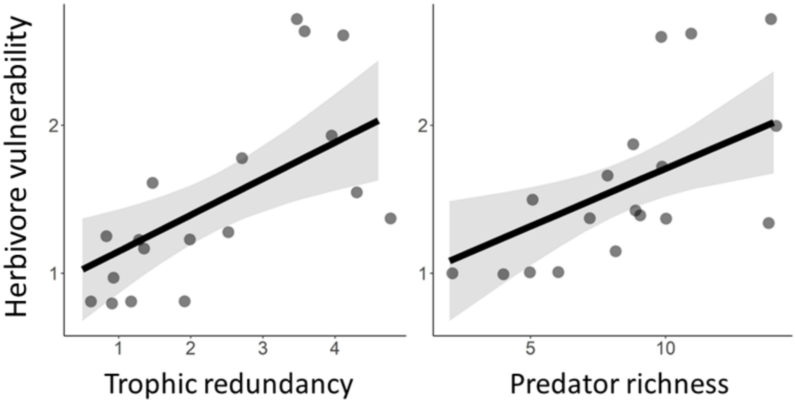


Figure 10. Relationship between predator trophic redundancy, predator richness and the ecosystem service of herbivore regulation, measured as the vulnerability of herbivorous prey in trophic food webs (adapted **paper III**).

Although not presented in this thesis, additional predator exclusion cages were brought out into the fields, inoculated with aphids, and after aphid establishment, were opened to assess aphid predation by predator communities dwelling in fields (communities dwelling in crop fields were assessed and analysed in paper I). Using predator exclusion cages, I find the same positive relationship of increased herbivore regulation, measured as the percentage decrease in aphid numbers over time, with increasing diversity of predator communities similar to the trophic interaction networks (Figure 11).

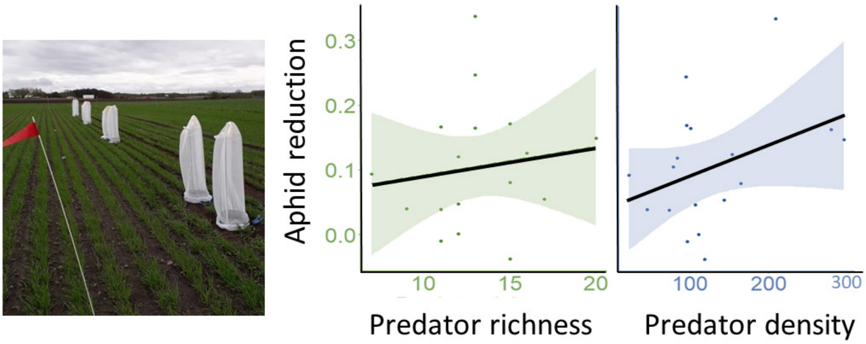


Figure 11. Relationship between predator richness or predator density and the reduction of inoculated aphids in predator exclusion cages in Halland County, south-western Sweden, 2020.

Similar patterns in dietary analysis and exclusion cages confirm that predator richness predicts pest control, emphasising the link between biodiversity and ecosystem function in arable fields. What is more, I find even stronger positive relationship between the aphid reduction and the abundances of predators (Figure 11), whereas predator abundance in fields sampled with the pitfalls did not emerge as the best predictor of pest control in the dietary analysis (**paper III**). The assessment of pest reduction over time by monitoring the decrease in aphid abundances does not allow establishing direct links between a predators' species and the pest consumed. That being said, the effect of other important arthropods such as ladybirds (known aphid predators) are included, but were not assessed in the measure of predator abundance in pitfall traps. Although we cannot establish a direct link between the predators and the prey, it is possible that the same habitat conditions attracting abundant ground dwelling predator communities into fields would also sustain other predators (e.g. ladybirds) contributing to pest regulation in open fields. In contrast, the dietary analysis presented in this thesis considered the gut contents of known carabid predators and their explicit links to the prey; thus, results might differ across methods. Incorporating both abundance and diversity and explicit links in predators' guts is challenging, but should be considered in the future.

5. Conclusion and future perspectives

The transition to sustainable agriculture depends on our understanding of how management interferes with the ecological relationships between species as well as species and their environment in arable fields. Within my thesis, I compared arthropod communities across intensities of agricultural management with the goal of identifying practices that benefit biodiversity in arable fields. I demonstrate that lowering the disturbance through management boosted the density and richness of arthropods above- and belowground, despite complex effects across various taxa and across diversification practices. Arthropods may benefit from lesser disturbance due to improved habitat and resource continuity. The latter, was provided by within-field available belowground prey sustaining predators cross the crop growing season. The richness of aboveground arthropod predator communities in turn, increased the predation pressure on herbivores. However, various prey resources across time were needed to foster species-rich arthropod predator communities, ultimately determining pest regulation.

My findings demonstrate that increasing biodiversity in arable fields can be facilitated by diversifying agricultural management. Reduced disturbance can boost the possibility for self-regulation in fields, with abundant and diverse arthropod communities minimising the need for herbivore regulation with pesticides. This is important if we wish to farm sustainably without the reliance on external inputs. By discussing diversification and its impact on ecologically interconnected communities in open fields and throughout the crop growing season, I provide knowledge to inform farmers and agricultural practitioners about which management practices could help nourish and protect the crops. This has direct applied relevance under the current ban of many agrochemicals in the European Union.

More farming practices can be evaluated for their impact on beneficial arthropod communities using the proposed general principles of habitat and resource continuity. This could serve as a principle for the development of additional diversification strategies in agricultural management supporting the goal of identifying also combinations of practices that benefit biodiversity in fields. For a full picture however, combined ecological and economic assessment would be needed to better address the economic risks and advantages for farmers associated to changes in management. From an ecological perspective, the long-term benefits of conserving biodiversity in fields are evident, but interests and needs of farmers might operate on other time scales and transitioning might entail large immediate costs. In order to facilitate the shift to more sustainable agricultural practices, we need to evaluate the short-term expenses, long-term savings, and develop strategies on how short-term financial risks might be shared among members in society.

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Popular science summary

One day on your way to the supermarket, you might have passed by an arable field. You may have wondered what the farmer grows there – and you may even have made the connection that you could, at some point, be eating the crop that you just saw. Most likely, you were not thinking about the insects and their important roles in these fields. Escaping our eyes, many so-called beneficial insects live in and on the soil, dwell in the crops and form a network of helpers that support crop growth. They can be small, like springtails living in the soil, but they can also be larger, like beetles roaming the soil surface on the search for prey. These beneficial insects have added value for crop production, as they are involved in breaking down organic materials, which then become available to crops. They also assist the farmer by feeding on other, herbivorous insects, thereby lowering crop losses by regulating pests. By doing so, beneficial insects have the ability to replace external inputs and make crop production more sustainable. But from a research perspective, there is still much work to be done, as we need to identify the management practices that best foster communities of such insects.

Current crop management causes disturbances through the turning of the soil (tillage), harvest, and low diversity of crops rotated in fields. Since such management practices may also cause a decline in the numbers of beneficial insects, crop yields are currently heavily dependent on the use of chemical fertilisers and pesticides for crop growth and protection. However, such management can easily turn into a vicious cycle, as it will pose further threats to the beneficial insects in these arable fields. For the last few decades, chemical interventions have been the method of choice, and have increased yields at the cost of insect biodiversity. The need for protecting insects through reducing the application of chemicals has now been recognised by the European Union, which has impended a ban on many pesticides. However, to prevent new crop losses, we need to better understand how we can support the beneficial insects already in place. This we can do by tuning agricultural management practices to help farmers protect their yields in more sustainable ways.

My thesis aims at identifying within-field management practices that help support beneficial insects and thus conserve the important functions that they provide. This is a challenging task, as first, we need to identify the impact of agricultural management on habitat conditions within the fields, and second, we need to assess whether these modified conditions align with the ecological needs of the beneficial insects (i.e. whether they can provide the food, shelter and partners needed by insects). Adding to the complexity of the task, we need to consider whether these insects show different dynamics (i.e. changes in numbers or diversity) over time. Insects have various life stages that may be susceptible to different aspects of management. For example, some adult insect may move between fields in pursuit of changes in available resources over time. Additionally, we cannot think of insects above and below ground as being isolated from each other. Instead, they may be linked through feeding interactions between predators and prey – of which the latter may hide under the soil surface. The combination of all these factors creates many challenges for understanding and connecting the effects of management on functions derived from insect communities.

To consider some of these complexities in my work, I designed field studies aimed at shedding light on the intertwined aspects of insect communities. I studied the effect of different intensities of soil turning, or the use of organic fertiliser, in combination with or without perennial grasses, as strategies for boosting ecosystem functions. Overall, we should clearly aim to decrease the disturbance imposed by management, but increase food and shelter for beneficial insects. These practices are referred to as "diversified management", as they aim at diversifying the conditions and insect communities in arable fields. To specifically address linkages between above- and belowground insects, I mapped out their feeding interactions drawing on molecular gut content analysis. Furthermore, I investigated the impact of diversified management on overwintering life stages, by pinpointing the contribution from overwintering predators to the overall communities assembled in fields. And most importantly, I addressed management impacts on insect communities throughout and across the crop growing season. By this versatile approach, I aimed to track changes in these communities over time, and to link legacies of management to the ability of the communities to recover after disturbance.

I found that beneficial insects above and below ground increased in numbers and diversity with less intensive management. Both aspects have important impacts on the services that these communities provide. By drawing on molecular gut content analysis, I found that diverse predator communities exert stronger control of herbivorous pests. These effects arise from more species feeding on each crop pest species, thus increasing overall predation pressure. At the same time, my analyses revealed that above- and belowground communities are inextricably linked through feeding interactions between predators living above ground and prey living in the soil. Specifically, I found that soil prey can sustain diverse predator communities in early season, providing an unbroken resource supply to predators. Furthermore, I showed that increased turning of the soils decreases the numbers and diversity of species communities, by altering the complexity of species' habitats (i.e. by reducing remaining plant residues and soil moisture). Insect communities above and below ground recovered at different pace from disturbance, with the time to recovery varying with how severely the turning of the soil and the thus-created disturbance had affected species' ecological requirements. For example, spiders – which depend on plant residues for attachment of their webs – were affected for a longer time, whereas ground beetles – which show less specific habitat needs – recovered more quickly. I found little impairment of overall overwintering communities with the turning of the soil, my finding of similar overwintering densities illustrates that the timing of management needs to align with species-specific life-cycles and if that is given, might not impact communities severely. However, I also discovered that habitat management can create legacy effects lasting over several years, with changes in communities being detectable well after 3 years. This finding highlights that many management effects accumulate and potentially worsen over time, but also that lowering management intensity can have positive effects for many years.

In my thesis, I demonstrate that the diversification of agricultural practices holds great potential for strengthening populations and communities of beneficial insects in crop fields, by providing habitat and resource continuity. To harness the biodiversity generated services from beneficial insect communities, I recommend farmers to extend their crop rotations with perennial grasses and to reduce the intensity of soil-turning in fields. Overall, I suggest that we need to start treating and managing arable fields as biodiverse habitats, and to do so at a landscape level. Overall, I want to imagine a future where arable lands are buzzing with insects and where we cherish the interactions that make up the whole ecosystem that we so heavily depend upon. Maybe you will share my vision on your next trip to the supermarket?

Populärvetenskaplig sammanfattning

En vacker dag när du var på väg till din lokala butik för att handla, passerade du kanske en åker. Du kanske undrade vad det var för gröda som bonden odlade, ja du kanske till och med tänkte tanken att, en dag, skulle just den gröda som växte här ligga på din tallrik. Troligtvis tänkte du nog inte på de insekter som levde i åkern och den roll de spelade i hur grödorna växte. På och i åkermarken, bortom vårt vardagliga synfält, bor och verkar en mångfald av nyttoinsekter som tillsammans bildar nätverk av medhjälpare som främjar grödornas tillväxt. De kan vara små, som hoppstjärtarna vi finner inne i jorden, men också större, som de skalbaggar som strövar omkring på markytan i jakt på ett byte. Dessa nyttoinsekter tillför mervärden för växtproduktion eftersom de bryter ner organiska ämnen som sedan blir tillgängliga för växterna att ta upp. De hjälper också bönder genom att livnära sig på andra växtätande insekter, och minskar därför risken för skördebortfall på grund av skadedjur. På så sätt kan nyttoinsekter bidra till att minska externa insatsmedel och göra växtodling mer hållbart. Ur ett forskningsperspektiv återstår dock mycket arbete, eftersom vi behöver identifiera vilka odlingstekniker som bäst främjar förekomsten av nyttoinsekter.

Nuvarande odlingstekniker förorsakar störningar genom jordbrytning (plöjning), skörd och en låg mångfald av odlade grödor. Eftersom dessa odlingstekniker också kan leda till en minskning av antalet nyttoinsekter förblir den resulterande växtproduktionen tungt beroende av kemiska insatsmedel som mineralgödsel och bekämpningsmedel för stabila skördar. Detta kan i sin tur skapa en ond spiral, då kvarvarande nyttoinsekter i åkern därmed hotas ytterligare. Under de senaste årtiondena har användningen av kemiska insatsmedel varit det dominerande tillvägagångssättet, och dessa har ökat skördenivåerna på bekostnad av biologisk mångfald. Nödvändigheten av att skydda insekter genom att minska andelen kemiska insatsmedel har dock numera erkänts inom EU, och resulterat i restriktioner eller regelrätta förbud mot deras användning. Det finns emellertid ett stort behov av fördjupad kunskap om hur vi kan främja de nyttoinsekter som redan finns i åkern för att undvika eller minimera skördeförluster, genom att t.ex. förbättra rådande odlingstekniker på ett hållbart sätt.

Syftet med denna avhandling är att identifiera odlingstekniker som bidrar till nyttoinsekters främjande, och därmed även till främjandet av de viktiga funktioner de utför inom växtproduktion. Det är en rejäl utmaning eftersom det innebär att vi först måste identifiera effekterna av de olika odlingsteknikerna på insektshabitatet inom en viss åker, för att sedan utvärdera hur dessa förändringar i sin tur påverkar ekologiska preferenser och behov hos nyttoinsekterna (dvs huruvida de kan tillgodose behoven av föda, skydd och partner). Inte nog med det, vi måste även beakta hur insekterna påverkas (dvs hur deras abundans eller mångfald förändras) över tid. Insekter genomgår flera olika livsstadier som alla kan innebära varierande grad av känslighet mot olika odlingstekniker. En viss typ av adulta insekter kan till exempel behöva röra sig mellan åkrar i takt med att födotillgången förändras över tid. Vi kan dessutom inte tänka på de insekter som vistas ovanför marken som isolerade från de som lever inne i jorden, eftersom de kan vara sammanlänkade i födovävsinteraktioner mellan predatorer och byten, där t.ex. de senare kan ta skydd under markytan. Sammantaget innebär kombinationen av faktorerna ovan en betydlig utmaning för vår förståelse och förmåga att länka samman effekterna av växtodling på åkerlevande nyttoinsekter och deras härrörande ekosystemfunktioner.

Med ovanstående utmaningar i åtanke, utarbetade jag en fältstudie med syfte att kasta nytt ljus på de olika men sammanlänkade aspekterna av insektssamhällen. Jag undersökte olika hur grader av plöjningsintensitet eller användandet av stallgödsel i kombination med eller utan inslag av perenna gräs lämpade sig som strategier för att öka ekosystemfunktioner. Uppenbart är att vi bör försöka minska graden av störning länkade till odlingstekniker, medan vi bör öka mängden föda och habitat för nyttoinsekter. Konkret kallar vi sådana bruksmetoder för ”diversifierade odlingstekniker”, eftersom de ämnar öka mångfalden av både nyttoinsekter och förutsättningar och deras förutsättningar i åkermark. För att specifikt studera länken mellan insekter ovanjord och i marken kartlade jag födointeraktioner genom molekylära analyser av maginnehåll. Jag undersökte dessutom effekten av diversifierade odlingstekniker på insekters livsstadier under övervintring genom att studera länken mellan övervintrande predatorer och sammansättningen av bredare insektssamhällen. Kanske viktigast av allt är dock att aspekterna ovan undersöktes över både enstaka och flera efterföljande växtsäsonger. På så sätt kunde jag följa förändringar över tid, men även knyta långvariga effekter av odlingstekniker till insekternas förmåga att återhämta sig efter störningar.

Mina resultat visar att minskad odlingsintensitet ledde till en ökad mängd och mångfald av nyttoinsekter, vilka båda är fundamentala komponenter i de tjänster som insekterna förser oss med. Molekylära analyser av maginnehåll visade att en mångfald i grupperna av predatorer leder till starkare reglering av skadedjursinsekter. Dessa effekter härrör ur att det för varje art av skadeinsekter även finns flera arter av predatorer, vilket ökar det totala predationstrycket. Samtidigt visar resultaten att insektssamhällen ovan- och i marken är tätt sammankopplade genom födovävsinteraktioner mellan predatorer på markytan och deras jordlevande byten. Genom att utgöra en stabil tillgång på föda kan de insekter som bor i marken upprätthålla predatormångfald tidigt under växtsäsongen. Om sedan plöjningsintensiteten höjs, minskar därmed även mängden och mångfalden av insekter genom en minskad habitatskomplexitet (dvs. mängden växtrester och markfuktigheten minskar). Tiden det tog att återhämta sig från störning skiljde mellan marklevande insekter och insekter på markytan, och varierade beroende på plöjningstrycket och hur störningen påverkade arternas preferenser och behov. Spindlar, till exempel, är beroende av växtmaterial som fästpunkter för sina nät och påverkades under lång tid av störningar, medan jordskalbaggar som har färre specifika habitatsbehov återhämtade sig snabbare. Överlag fann jag få effekter på övervintrande arter efter plöjning, och de jämförbara mängderna av dessa grupper visar på att om insatsen som leder till störning tajmas med arternas specifika livscykler kan större skadeverkningar undvikas. Effekten av brukningsmetoder kan emellertid verka över lång tid, då jag fann att förändringar i insektssamhällen kvarstod efter tre år. Detta resultat understryker det faktum att många störningseffekter kan ackumulera och förvärras över tid, men även att en minskad brukningsintensitet kan ha positiva följdeffekter över flera år.

I min avhandling visar jag att diversifieringen av odlingstekniker i växtproduktion har stor potential att främja samhällen och populationer av nyttoinsekter i åkermark genom att tillgodose habitat och födokontinuitet.

För att bäst dra nytta av de ekosystemtjänster som genereras av en mångfald av nyttoinsekter är min rekommendation till bönder att utöka växtföljder med perenna gräs och att minska plöjningsinsatsen. På det stora hela anser jag att vi bör sköta våra åkermarker som särskilt artrika habitat, och att detta perspektiv även utökas till att inkludera hela landskapet. Jag vill kunna föreställa mig en framtid där åkermarkerna kryllar av insekter, och där vi uppskattar och värdesätter de interaktioner som tillsammans utgör ekosystemen vi är så beroende av. Kanske delar du lite av samma dröm nästa gång du åker till butiken och handlar?

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Unterstützung und unerschütterliche Motivation mir alles über Milben beizubringen.

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Combining organic fertilisation and perennial crops in the rotation enhances arthropod communities

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ABSTRACT

Single and combined diversification practices in crop fields and their effects on arthropod predators, decomposers and herbivores have mainly been assessed in small plot and cage experiments. In particular, effects of diversification on arthropod predators and their food resources, such as soil fauna, weed seeds and herbivorous prey in entire crop fields across the growing season, remain unclear. We explored how organic fertilisers, with or without the legacy of perennial ley in the crop rotation, and mineral fertiliser without the legacy of perennial ley, affected below- and aboveground communities in 19 spring cereal crop fields. In each field, we determined the abundance of the soil mesofauna, communities of arthropod prey aboveground and of the predator guilds carabids, staphylinids and spiders. We sampled at three crop stages: tillering, heading and ripening. Weed cover and soil characteristics, such as carbon and nitrogen content, were assessed. For most soil mesofauna groups, the combination of organic fertiliser with the legacy of ley gave highest, organic fertiliser with annual crop rotations intermediate, and mineral fertiliser with annual crop rotations the lowest total abundance. Aboveground arthropod prey abundances were similar across treatments. The legacy of ley increased richness of all aboveground arthropod predators. Staphylinid communities' abundance increased additively as diversification treatments were combined during tillering of the crop. Increasing organic amendments, alongside the reduced disturbances through inclusion of perennial ley in the rotation, led to more abundant communities below- and aboveground as well as more richness in aboveground predator communities.

1. Introduction

Intensive farming includes monoculture cropping systems dominated by high yielding crops in short rotations (Aguilar et al., 2015; Bennett et al., 2012) from which perennial grass-legume mixes and organic fertilisers often historically have been removed (Garrett et al., 2020; Martin et al., 2020; Naylor et al., 2005; Picasso et al., 2022) This has weakened the provisioning of ecosystem services such as biological pest regulation, soil fertility and nutrient cycling (Albizua et al., 2015; Dainese et al., 2019; Tamburini et al., 2020). (Re)-diversifying agriculture is suggested as a way to reverse these negative trends without penalising yields (Bommarco et al., 2013; Kremen and Merenlender, 2018; Kremen and Miles, 2012; Tittonell, 2014). Effects of single practices on single or few factors have been tested (Tamburini, 2020) but knowledge of outcomes of combined diversification practices on biodiversity and ecosystem functioning is still missing.

Crop field diversification practices include the use of organic amendments (Kremen and Miles, 2012; Tamburini et al., 2020) and perennial ley in crop rotations (Lemaire et al., 2015; Martin et al., 2020). Leys are mixes of perennial legume and grasses incorporated into crop rotations for feed production and fallow. Both practices enhance and maintain soil organic carbon pools (Scotti et al., 2015), which can promote local communities of beneficial organisms above- and belowground (Eyre et al., 2012; Marrec et al., 2015; Palmu et al., 2014; Tsiafouli et al., 2015). Short term plot experiments show that the diversification practice of adding organic fertilisers can support diverse and abundant communities of beneficial arthropods such as carabid beetles (Aguilera et al., 2020), but there are few examinations of combining this with other diversification practices (Tamburini et al., 2020). For instance, combining organic fertilisation and perennial leys in crop rotations, increases soil organic matter (SOM) and improves soil aggregation, providing complex habitats for soil fauna (Emmerling et al., 2021; Haynes, 1999). These effects could persist despite perturbations from annual cropping in subsequent years. Combined diversification might build abundances of below- and aboveground communities, which underpin ecosystem services such as pest regulation

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and nutrient cycling in crops following ley, but this remains to be tested for predators, herbivores and decomposers above- and belowground in arable fields and across the season.

Soil organisms in crop fields provide a number of ecosystem services that support crop production, such as decomposition, nutrient cycling and water regulation (Barrios, 2007; Kulmatiski et al., 2014). Soil food webs break down organic matter and release nutrients to the crops enhancing use efficiency of nutrients and reducing the need of mineral fertilisation (Bardgett and Chan, 1999). Organic fertilisers can increase soil diversity (Lin et al., 2019; Liu et al., 2016; Lori et al., 2017) and abundance of several taxa (Axelsen and Kristensen, 2000; Riggi and Bommarco, 2019). Benefits on abundance and diversity of soil organisms are, however, dependent of the quality of organic fertilisers applied (Viketoft et al., 2021). Perennial leys in crop rotations increase carbon and nitrogen content in the soil, improve its chemical and physical properties (Hoeffner et al., 2021) and benefit abundance and diversity of soil fauna communities (Crotty et al., 2016; Emmerling et al., 2021). Positive effects on abundance and diversity of soil organisms persist for several years after the transition from perennial leys to annual arable crops (Crotty et al., 2016). These legacy effects have been associated with lower disturbance of the soil with perennial crops (Lemaire et al., 2015) and increased habitat complexity through altered soil structure mediated by greater root development compared with annual crops (Marshall et al., 2016) and addition of SOM to the soil (Hernanz et al., 2009).

Organic fertilisers can enhance soil fauna abundance which constitutes a food resource for predatory arthropod communities above ground that contribute to the suppression and population regulation of crop herbivores (Birkhofer et al., 2008; Holland and Luff, 2000). Strengthened predator communities via increased availability of belowground prey has in short term plot experiments been seen to result in top-down suppression of aphid population abundance compared with mineral and no fertilisation (Aguilera et al., 2021; Riggi and Bommarco, 2019). The pest suppressive effect depends on fertiliser type and its quality to the soil fauna and herbivores (via impacts on plant quality) (Riggi and Bommarco, 2019). It remains unknown whether the top-down regulation effects are maintained across entire seasons and crop fields. Increasing alternative prey to predators via organic fertilisation could suppress pest populations by decoupling predator populations from dependence on only herbivores as prey. Prey communities generally fluctuate during the cropping season and if belowground prey is accessible already early in the season, this could stabilise aboveground predator communities at a time when herbivorous prey has not yet colonised the crop. The cascading effects of organic amendments on natural enemies' communities have to our knowledge not been quantified in multiple fields across the season.

To assess the effect of legacies of single and combined diversification practices on both soil mesofauna and aboveground arthropod predator and prey communities in arable fields, we compared three diversification practices: annual crop rotations receiving either mineral or organic fertilisers, and fields rotated with perennial ley receiving organic fertilisers. All farms in the region that had perennial ley in their crop rotation also applied organic fertiliser such that the combination of mineral fertilising and ley in rotation was not available. We sampled from early tillering of the crop until shortly before harvest to capture effects across crop development stages. We hypothesised that (1) adding organic fertilisers to a rotation with annual crops increases the abundance of soil mesofauna compared with fields receiving mineral fertiliser, (2) incorporating ley in the crop rotation further increases the soil fauna abundances, and (3) the abundance and diversity of aboveground arthropod predator communities increase as a result. We further expected, (4) no interactions among treatments and crop stages for soil mesofauna as they are locally bound to the fields, whereas (5) there is an interaction between treatment and crop stage for aboveground arthropod predator communities. The latter is due to aboveground predators colonising diversified fields at an earlier crop stage, as prey is already available in the form of soil fauna. During late crop stages, we expected aboveground arthropod predator communities to become more similar in abundance and diversity among treatments, as all fields provide a wider array of available prey to sustain aboveground predator communities.

2. Material and methods

2.1. Study area and site selection

We selected 19 conventionally managed fields with spring-sown cereals (oats and barley) located in Halland county along the SW coast of Sweden (56.85° N, 12.85° E). The county is dominated by agricultural crop and animal production with high productivity due to ample annual rainfall of 700–800 mm and long days in the growing season. Sampling of above- and belowground arthropod communities was carried out during three crop stages in 2020, at tillering (early May, approx. 20 days after sowing), during heading (early June) and during early ripening (early July). Crop stages were assessed according to Large (1954). Prior to our experiment, fields differed in their crop rotation (see additional information on crop rotations in Table A.1) and received either mineral or organic fertilisation. Treatments included fields that only received mineral fertiliser and were rotated with annual crops (FminRa; n = 6), fields treated with organic fertilisers (manure and slurry, see Table A.2) rotated with annual crops (ForgRa; n = 7) and fields treated with organic fertiliser where crop rotation included 3 years of perennial leys (ForgRl, n = 6). All farms in this region with perennial leys in their crop rotation applied organic fertilisers, such that the design could not be fully crossed. The fields were managed under the respective treatment for a minimum of six years. At sampling, fields rotated with ley had been without ley for at least two years. We thereby captured legacy effects instead of immediate pre-crop effects. All fields were ploughed regularly. Crops were sown between 7th and 15th of April 2020. To control for comparable conditions for soil mesofauna sampling, soil texture was assessed based on farmer's knowledge of their field and balanced across treatments. Soil textures were later formally confirmed using the soil composite samples for soil content analysis (see additional information Table A.1 and Section 2.6). Crop rotation information was obtained through farmer questionnaires and the Integrated Administration and Control System (IACS), administered by the Swedish board of Agriculture.

To verify that treatments were not affected by the surrounding landscape composition, we calculated the percent of arable land and forest in a 500 m radius around each study site as both represented dominant habitat types in this region. Calculations were based on digital land cover maps (Terrängkartan, Lantmäteriet, 2018, IACS). We found that the proportions of the landscape characteristics were balanced across treatments (Table A.1).

2.2. Experimental set up

In each field, we set up a sampling area of 25 × 50 m after sowing in which no insecticides were applied in agreement with the farmers. Herbicides and fungicides were applied in the sampling area same as in the rest of the field according to each farmers individual decision. The sampling areas were placed either at the field border or inside the field depending on farmer's need and soil type. The placement of the sampling area at the border or inside the fields was balanced across treatments (see Table A.1). Sampling took place along two 30 m long transects with four sampling points in each. To avoid the effect of insecticide spray drift, transects were placed at 8 and 14 m from the border of the sampling area (Figure A.1). The same sampling effort was applied in all fields allowing for relative comparisons of communities among fields.

2.3. Soil mesofauna community sampling

Soil mesofauna was sampled by taking four intact soil cores (5 cm diameter and 10 cm depth) per field at all three crop stages. Soil core sampling with subsequent extraction is a widely used method for estimating soil mesofauna occurrences (e.g., González et al., 2021) robust to biases from other techniques that often fail to capture less mobile species. Soil cores were taken at two sampling points per transect and refrigerated at 4 ºC until Tullgren extraction (Tullgren, 1918). The extraction lasted for four days with a gradual increase over the first 24 h to a target temperature of 52 ºC that was held constant for the remaining 72 h. All collected soil mesofauna was preserved in a glycol-ethanol solution (80 % ethanol) until sorting in the lab. Individuals were counted and assigned to the following five groups: Collembola, Mesostigmata, Oribatida, juvenile Acari, and other arthropods (individuals >2 mm, e.g., millipedes).

2.4. Aboveground arthropod predator community sampling

In each transect, we placed four pitfall traps, approximately 3.5 m apart, resulting in eight pitfalls per field. Plastic cups (12 cm diameter, 12 cm deep) were placed into the soil and filled with approximately 200 ml of water with added odourless detergent. During each crop stage sampling, pitfall traps remained open for four consecutive days. Operating pitfalls over a set period allows adequate assessment of mobile predators, as they capture a large number of invertebrates, removing biases in abundances of rare specimens arising from one-time snapshot sampling. Collected specimen were stored in 70% ethanol and identified in the lab. All spiders and carabid beetles were identified to species, staphylinid beetles to genus.

2.5. Aboveground arthropod prey community sampling

Aboveground arthropod prey communities were sampled during mid and late crop stage when the crop had grown enough for herbivores to establish in the crop and allowing for sampling them with sweep nets, which was not possible in the early crop stage. Sweep netting hereby samples organisms dwelling on the crop or flying within the crop canopy allowing adequate assessment of the relative amount of available prey for predators. Two corridors for sweep netting were established in 1 m distance to the pitfall track transect to avoid interference with the pitfall traps. Along the two sweep netting transects, four sweeps with 15 strikes each were taken. Caught insects were transferred into plastic bags and stored in the freezer before storing them in 70 %-ethanol up until identification.

Individuals were counted and compiled within the following three groups: flies, small herbivores and large herbivores. Flies included Diptera belonging to the suborder or families Syrphidae, Chloropidae, Brachycera and Nematocera. Small herbivores (<2 mm) included Aeolothripidae, other Thysanoptera and Aphidoidea. Large herbivores included Apionidae, Curculionidae and Miridae.

2.6. Soil content sampling

We took five soil cores (5 cm diameter, 10 cm depth) and pooled them into one composite sample per field. Sampling took place once during early crop stages. Samples were analysed for soil organic matter (SOM), total nitrogen and total carbon contents (https://www.agrilab.se).

To assess soil moisture, eight soil core samples (2.5 cm diameter, 10 cm depth) were taken during each sampling round in early, mid and late crop stage near each pitfall trap. Samples were weighed before and after drying in the oven at 80 ℃ for 24 h. Soil moisture was assessed as the percentage difference in weight.

2.7. Community metrics

To characterise community differences among treatments, we calculated the abundance caught separately for each of the five soil mesofauna groups, the three aboveground arthropod prey groups as well as activity density of predators from the pitfall traps (hereafter: total abundance). Total abundance was defined as the number of captured individuals per field and crop stage by summing up the number of individuals caught in each replicate sample separately for each organism group. Therefore, total abundance is relative to the sampling method but comparable between treatments. Non-transformed total abundance of soil mesofauna was used in all analysis. For the visual presentation in `Fig. 1`, soil fauna abundances were re-scaled to the unit of individuals per m^2 in order to simplify comparability with other studies that most often present results from this sampling method in that unit.

Predator richness and Shannon diversity were calculated separately for the three predator groups of carabids, staphylinids and spiders. Predator richness was defined as the number of recorded species (carabids and spiders) or the number of recorded genus (staphylinids) per field and crop stage summed across replicate samples within each field and calculated separately for each organism group. Shannon diversity was calculated using the Shannon- Wiener index, where pi describes the proportion of the entire community made up of species i.

$$H = -\Sigma pi * \ln(pi)$$

All calculations were made within the “vegan” package (Oksanen et al., 2020).

2.8. Statistical analysis

2.8.1. Species communities

Generalised linear mixed models were used to assess the effect of diversification treatments (FminRa, ForgRa and ForgRl) and crop stage on the community metrics: i.e., total abundance for the five soil mesofauna groups and three aboveground arthropod prey groups as well as total abundance, predator richness and Shannon diversity for carabids, staphylinids and spiders. Individual models were fitted for each community metric and predator group. Each model included the interaction between diversification treatment and crop stage as fixed factors and field identity as random factor. We first built full models and then simplified them by removing non-significant ($p > 0.05$) interaction terms. We always kept the single terms, as they were part of the experimental design. Models on soil mesofauna abundances were fitted using non-scaled data referring to the non-transformed total abundance per field and crop stage. To achieve optimal model fit for small herbivores, we had to further simplify the model by dropping the random effect of field identity. To test the effect of sampling areas being located at the border or the inside the field, we included sampling area location as a random effect crossed with field identity. However, sampling area location did not explain any further variation and was therefore excluded.

Normal- or negative binomial distribution were used, depending on the distribution of residuals in each analysis. Error distributions were chosen to obtain optimal model fit (see 2.8.3 Model assumptions and fit) with negative binomial distribution for all mesofauna, aboveground arthropod prey and aboveground arthropod predator total abundance models and normal distribution for aboveground arthropod predator predator richness and Shannon diversity.

2.8.2. Soil quality analysis

Linear models were used to assess the effect of diversification treatments on the soil metrics.

soil organic matter, total nitrogen and total carbon contents, with treatment as a fixed factor. Individual models were fitted for each of the soil metrics. The effect of treatments on soil moisture was tested using a generalised linear mixed model. The interaction between diversification

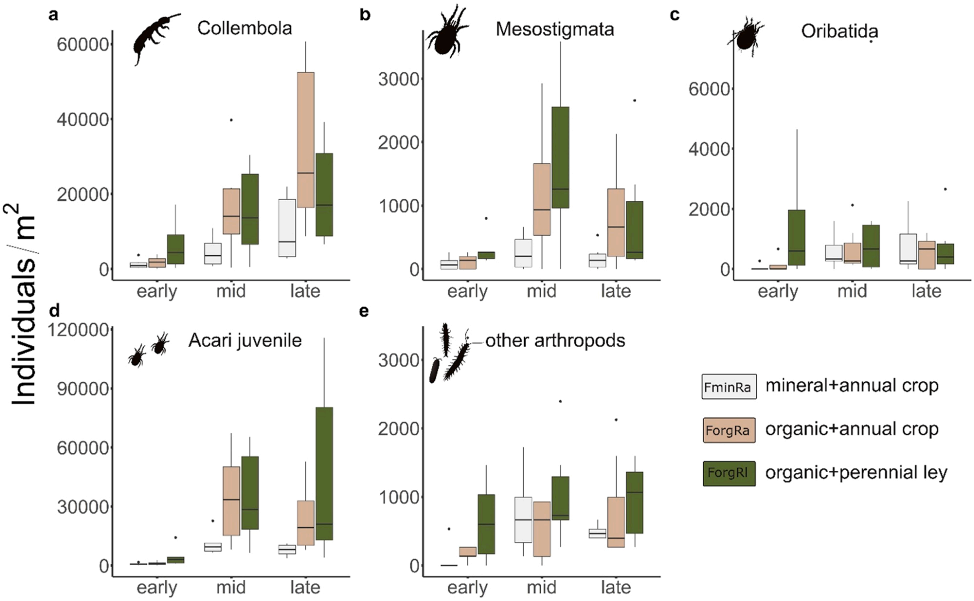

Fig. 1. Total abundances expressed as the number of individuals per m ^{2} of the five soil mesofauna groups: Collembola (a), Mesostigmata (b), Oribatida (c), juvenile Acari (d) and other arthropods (e) for three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green) during early, mid and late crop stage.

treatment and crop stage was included as fixed factors and field identity as random factor. Normal distribution was chosen based on residuals of the model.

2.8.3. *Model assumptions and fit*

We checked and validated model assumptions and fit by testing for over- and underdispersion and visually inspecting residual diagnostics of scaled residuals simulated from the model fit, i.e., deviation from uniformity and observed against predicted residuals. We calculated conditional and marginal R^2 (Nakagawa et al., 2017) implemented in the "performance" package (Lüdecke et al., 2021). Parameter significance was tested using Type II-Wald chi-square tests. Estimated marginal means were obtained using a Tukey post-hoc test within the "emmeans" package version 1.7.2 (Russell and Lenth, 2022).

All data were analysed using R version 4.1.1 (R Core Team, 2020) and packages "glmmTMB" version 1.1.2.9000 (Brooks et al., 2017), "stats" version 4.1.1, "DHARMa" version 0.4.5 (Hartig, 2021), "car" version 3.0–12 (Fox and Weisberg, 2019).

3. Results

In total, we sampled 14,048 individuals of soil mesofauna, 17,787 aboveground arthropod predators and 13,330 individuals of aboveground arthropod prey. Collembola and juvenile Acari were the most abundant groups of soil mesofauna (37 %, 55 % respectively) followed by Oribatida (2 %), Mesostigmata (1.8 %) and other arthropods (2.2 %). Carabids and staphylinids were the most abundant predator groups making up 34 % and 41 % of all predators respectively, followed by spiders making up 25 % of all sampled predators. Aboveground arthropod prey were dominated by small herbivores (mainly Thysanoptera) with 78 % followed by flies with 20 % and large herbivores with 2 % of the overall community. Table 1.

Table 1
Test statistics with χ^2-value, degrees of freedom, p-value, marginal and conditional R^2 for each model test on the effects of treatment and crop stage on total abundance of the five soil mesofauna groups. Statistically significant ($p < 0.05$) results are in bold, trends in italic ($0.05 < p > 0.1$). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Tables A.5.1 and A.5.2.

	Response variable	Explanatory variable	χ^2	DF	p-value	R^2_m	R^2_c
Collembola	Total abundance	Treatment	5.948	2	*0.051*	0.575	0.886
		Crop stage	141.829	2	**< 0.005**		
		Treatment: crop stage	14.727	4	**0.005**		
Mesostigmata	Total abundance	Treatment	8.961	2	**0.009**	0.496	0.778
		Crop stage	34.333	2	**< 0.005**		
Oribatida	Total abundance	Treatment	2.187	2	0.335	0.391	0.698
		Crop stage	5.186	2	*0.074*		
		Treatment* crop stage	9.310	4	*0.053*		
Acari juvenile	Total abundance	Treatment	14.594	2	**< 0.005**	0.772	0.887
		Crop stage	207.949	2	**< 0.005**		
Other arthropods	Total abundance	Treatment	4.016	2	0.134	0.242	0.403
		Crop stage	7.267	2	0.026		

3.1. Soil mesofauna

Collembola, Oribatida and juvenile Acari were most abundant in fields with organic fertilisation and perennial leys (ForgRl), intermediately abundant in fields receiving organic fertiliser and annual crops (ForgRa) and fewest in fields receiving mineral fertiliser and annual crops in the rotation (FminRa; Table A.5.1, Table A.5.2, Fig. 1). Treatment effects on Collembola and Oribatida abundances were dependent on the crop stage (Table1) with additive effects of treatments found at both early and mid-crop stage for Collembola (Table A.5.2) and at early crop stage for Oribatida (Table A.5.2). The total abundance of Mesostigmata was enhanced in fields receiving organic fertiliser combined with ley compared with fields receiving mineral fertiliser combined with annual crop rotations (Fig. 1, Table A.5.1). The abundance of other arthropods was not affected by treatment but increased from early to mid-season (Fig. 1, Table A.5.1).

3.2. Aboveground arthropod prey

We found no difference in aboveground arthropod prey abundances among the diversification treatments for flies (Figure A.4.1, Table A.4), small herbivores (Figure A.4.1, Table A.4) and large herbivores (Figure A.4.1, Table A.4).

3.3. Aboveground arthropod predators

3.3.1. Total abundance

Total abundance of carabid beetles was only marginally affected by the treatments (Table 2) with lower abundances in ForgRa fields compared with both FminRa and ForgRl (Table A.5.1, Fig. 2). Carabid total abundances increased with the succession of crop stages (Table A.5.1, Fig. 2). The total abundance of staphylinids was explained by the interaction of treatment and crop stage (Table 2) with highest staphylinid abundances in ForgRl, intermediate abundances in ForgRa and lowest in fields with FminRa (Table A.5.2, Fig. 2) only during early crop season. The total abundance of spiders was explained by the interaction of treatment and crop stage (Table 2, Fig. 2). *Post hoc* comparisons showed higher abundances in FminRa and ForgRl than in ForgRa (Table A.5.2) in late crop stage.

3.3.2. Predator richness

Carabid species richness was explained by treatment and crop stage (Table 2, Fig. 2) with higher species richness in ForgRl fields compared to ForgRa (Table A.5.1) and marginally higher species richness in ForgRl compared with FminRa (Table A.5.1). Carabid species richness increased from early to late (Table A.5.1) crop stage. The genus richness of Staphylinids was explained by treatment and crop stage (Table 2, Fig. 2) with higher genus richness in ForgRl fields than in FminRa fields (Table A.5.1). Staphylinid genus richness gradually increased from early to late crop stage (Table A.5.1).

The species richness of spiders was explained by the interaction of treatment and crop stage (Table 2, Fig. 2) with increased species richness in ForgRl than in FminRa in early season (Table A.5.2).

3.3.3. Shannon diversity

There were no treatment differences for Shannon diversity of carabid communities, but Shannon diversity increased from mid to late crop stage (Table 2, Fig. 2, Table A.5.1). Shannon diversity of staphylinid communities was explained by both treatment and crop stage (Table 2, Fig. 2) with marginally increased Shannon diversity in ForgRl fields compared to ForgRa fields (Table A.5.1) and increased Shannon diversity in mid compared to both early and late crop stage (Table A.5.1). Shannon diversity of spider communities was explained by the interaction of treatment and crop stage (Table 2, Fig. 2). During early season, spider Shannon diversity was marginally enhanced in ForgRl compared with FminRa (Table A.5.2). The reverse effect was found in mid-crop stage with lower Shannon diversity in ForgRl fields compared with ForgRa and FminRa (Table A.5.2).

3.4. Soil quality

Soil organic matter (SOM), nitrogen as well as carbon content were explained by treatments (Table 3) and enhanced only under the combined diversification of organic fertiliser and perennial ley in crop rotation (Table A.2.1, Figure A.2.1). The difference in soil moisture was explained by the interaction of treatment and crop stage (Table 3). Fields under combined diversification with organic fertiliser and perennial ley in the crop rotation had higher soil moisture compared to both, fields with mineral fertiliser and annual crop rotations and fields with single diversification of organic fertiliser and annual crop rotation, during

Table 2
Test statistics with χ^2-value, degrees of freedom, p-value, marginal and conditional R^2 for each model tests on the effects of treatment and crop stage on the respective community response variables for the three predator groups. Statistically significant ($p < 0.05$) results are in bold, trends in italic ($0.05 < p > 0.1$). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Tables A.5.1 and A.5.2.

	Response variable	Explanatory variable	χ^2	DF	p-value	R^2_m	R^2_c
Carabids	Total abundance	Treatment	5.857	2	*0.053*	0.246	0.649
		Crop stage	9.974	2	**0.006**		
	Species richness	Treatment	10.613	2	**0.004**	0.308	0.589
		Crop stage	9.667	2	**0.007**		
	Shannon diversity	Treatment	2.098	2	0.350	0.149	0.149
		Crop stage	7.738	2	**0.020**		
Staphylinids	Total abundance	Treatment	3.614	2	0.164	0.466	0.539
		Crop stage	30.210	2	**< 0.005**		
		Treatment* crop stage	11.709	4	**0.019**		
	Genus richness	Treatment	7.236	2	**0.026**	0.388	0.515
		Crop stage	31.870	2	**< 0.005**		
	Shannon diversity	Treatment	4.735	2	*0.093*	0.262	0.332
		Crop stage	15.762	2	**< 0.005**		
Spiders	Total abundance	Treatment	4.996	2	*0.082*	0.351	0.533
		Crop stage	10.062	2	**< 0.005**		
		Treatment* crop stage	17.912	4	**0.001**		
	Species richness	Treatment	0.342	2	0.842	0.352	0.507
		Crop stage	25.919	2	**< 0.005**		
		Treatment* crop stage	13.532	4	**0.008**		
	Shannon diversity	Treatment	1.998	2	0.368	0.288	0.390
		Crop stage	7.870	2	**0.019**		
		Treatment* crop stage	15.640	4	**0.003**		

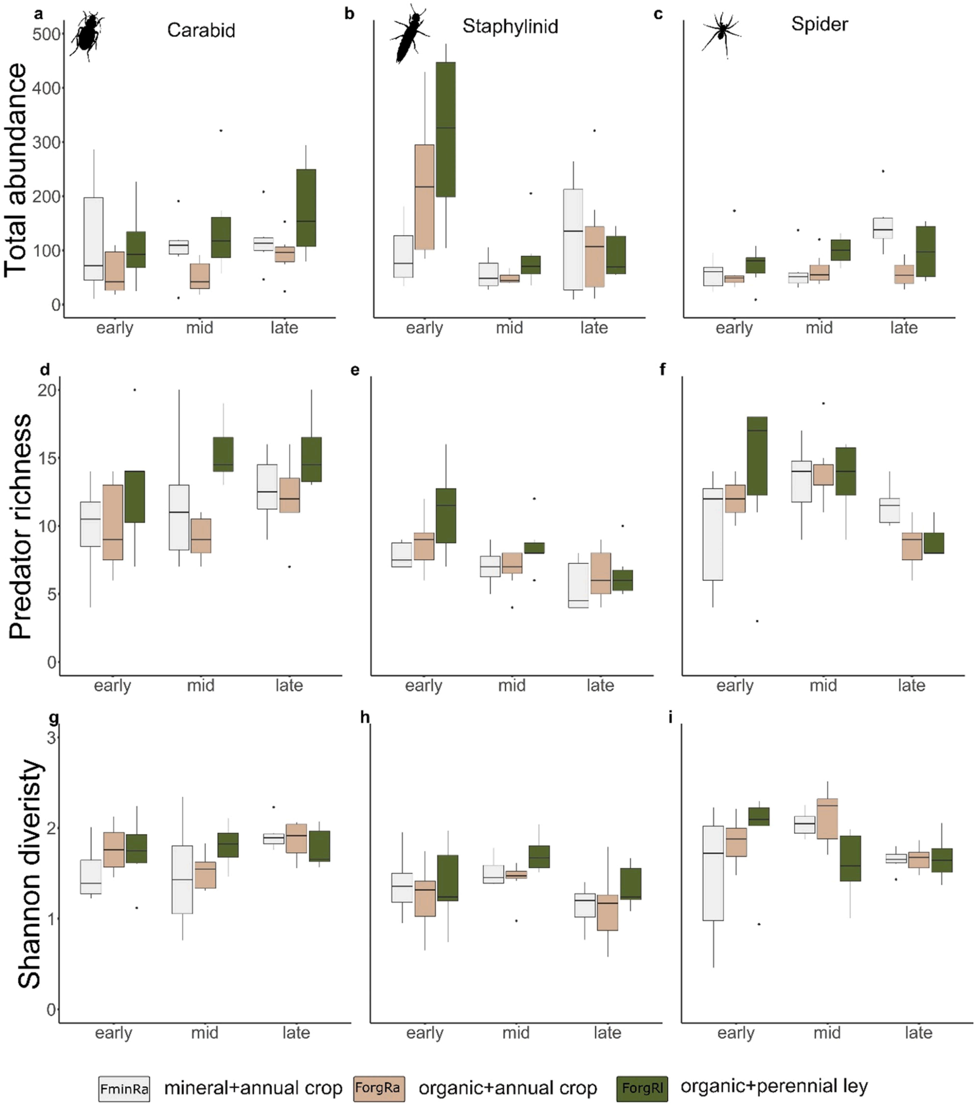

Fig. 2. Total abundance expressed as individuals caught per field using eight pitfall traps (a-c), predator richness (d&f=species richness; e=genus richness) and Shannon diversity (g-i) for the three natural enemy guilds carabids, staphylinids and spiders for the three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green) during early, mid and late crop stage.

early and mid-crop stage (Figure A.2.2, Table A.2.2).

4. Discussion

The combined effect of organic fertilisation and legacy of ley enhanced abundance of soil mesofauna and affected abundance, predator richness and Shannon diversity of some, but not all, aboveground arthropod predators. Community differences across treatments occurred mostly in the early- and mid-crop stages. In contrast to our expectations, we found no differences among treatments for the abundance of aboveground arthropod prey at any crop stage. Combining organic fertilisation and perennial ley in the crop rotation consistently enhanced SOM, nitrogen and carbon content and moisture in the soil.

Table 3
Test statistics with sum of squares (lm) or χ^2-value (glmm), degrees of freedom, p-value, marginal (lm, glmm) and conditional R^2 (glmm) for each model tests on the effects of treatment and crop stage on the respective community response variables soil organic matter (SOM), nitrogen- and carbon content as well as soil moisture of agricultural soils. Statistically significant ($p < 0.05$) results are in bold, trends in italic ($0.05 < p > 0.1$). Test statistics including pairwise comparisons of treatments reporting their estimates, standard errors (SE), t-ratio and p-values can be found in supplementary Table A.2.1.

	Metric	Explanatory variable	Sum of squares / χ^2	DF	p-value	R^2_m/R^2_c
Lm	SOM	Treatment	39.432	2	**0.002**	0.525/-
	Nitrogen content	Treatment	3.315	2	**0.008**	0.450/-
	Carbon content	Treatment	1075.0	2	**0.005**	0.482/-
Glmm	Soil moisture	Treatment	8.348	2	**0.0153**	0.48/0.952
		Crop stage	287.819	2	**$<$ 0.005**	
		Treatment*crop stage	23.550	4	**$<$ 0.005**	

4.1. Diversification effect on abundances of soil mesofauna

As expected, diversification increased the total abundance of soil mesofauna compared with annual crop rotation with mineral fertiliser (Viketoft et al., 2021). The highest abundances occurred when organic fertilisers and perennial ley in the crop rotation were combined. Only marginally statistically significant effects were apparent for some groups (e.g., Collembola) and for the single effect of organic fertiliser, but trends in effect sizes were consistent for all soil fauna groups.

Strong effects on soil mesofauna under combined diversification were expected as soil mesofauna depend not only on food resources, but also other niche dimensions such as disturbance and habitat quality (Coulibaly et al., 2022; Purvis and Curry, 1980). Long term fertilisation plot experiments showed variable effect of organic fertiliser on soil mesofauna abundances depending on fertiliser type and quality (Aguilera et al., 2021; Viketoft et al., 2021). Interestingly, our field study showed that soil mesofauna consistently benefited from the addition of organic fertiliser alone despite differences in fertiliser type among fields and low replication of study sites. Addition of organic fertiliser improves conditions for the mesofauna, most probably by increasing their food resources both in the form of organic matter but more importantly by increasing the microorganisms that colonise organic matter (Potapov et al., 2022). To assess the impact of diversification on microorganisms, soil microbial quality indicators such as total microbial biomass (C_{mic}) need to be measured which was not done in the present study. However, SOM was measured which gives an indication of microbial biomass C_{mic} constituting food resources for most microorganisms (Gentry and Zuberer, 2021). We therefore speculate that high amount of SOM under combined organic fertilisation and perennial crops likely resulted in higher mesofauna abundance.

We found that perennial leys in the crop rotation combined with organic fertilisers increased soil moisture (Figure A.2.2), potentially creating favourable habitat and microclimatic conditions for soil mesofauna (Franzluebbers et al., 2014; Yazdanpanah et al., 2013). Especially soft bodied organisms, such as Collembola and juvenile Oribatida and Mesostigmata, are prone to desiccation and dependent on sufficient soil moisture for reproduction and growth (Tsiafouli et al., 2005; Wang et al., 2022). Additionally, the lower disturbance associated with perennial leys in the rotation could contribute to enhancing soil mesofauna communities overall. Given that our fields had been without ley for two years prior to sampling suggests that such positive effects on soil mesofauna communities can persist for several years after the ley has been removed (Crotty et al., 2016). Farming practices that provide food and habitat for beneficial organisms show promise to enhance ecosystem services, such as decomposition, nutrient cycling and crop protection mediated by soil mesofauna.

4.2. Diversification effects on predators and prey

Despite consistent positive effects on soil mesofauna communities, treatment effects did not directly propagate to all aboveground predator groups. Staphylinid communities showed the hypothesised stepwise increase in abundances, with highest abundances under combined diversification with organic fertiliser and perennial ley, intermediate abundances under single diversification with organic fertiliser and lowest abundances in fields with mineral fertiliser, during early season. Predator richness was highest under combined diversification with organic fertilisers and perennial ley. Treatment effects on spider communities differed across crop stages with highest species richness during tillering of the crop in fields under combined organic fertiliser and perennial ley, but highest abundances in late crop session in fields receiving mineral fertiliser.

Various food resources are available in crop fields. We found abundances of aboveground herbivore and Diptera prey to be similar across treatments (Figure A.4) but alternative food resources differed among treatments. Fields with mineral fertilisers had higher weed cover, which could provide alternative food resources such as weed seeds, whereas fields with combined organic fertiliser and leys harboured higher soil fauna abundances (Fig. 1). Predators may be able to exploit these resources, which would explain the weak differences of carabid predator abundances between fields with mineral fertiliser in comparison to organic fertiliser in combination with perennial ley that we observed. This might affect the regulation of the herbivore populations positively if more generalist predators are sustained in the field or negatively if the predator community becomes dominated by other specialists, such as weed seedeaters that do not feed on herbivores.

Several species of arthropod predators are known to overwinter in agricultural soils and community build-up is negatively affected by cropping practices that disturb the soil and deplete soil organic carbon (Hanson et al., 2016; Holland et al., 2009). Positive effects of diversified practices, mainly through the inclusion of perennial leys, on staphylinid abundances occurring during early season, suggest that local build-up of communities could be facilitated by improved reproduction and overwintering success with reduced disturbance in the field (Martin et al., 2020). Comparisons between spring emergence in ley and cereal crop fields, showed lower dispersal tendency of staphylinids in ley fields suggesting that staphylinids tend to disperse less in undisturbed habitats (Hanson et al., 2016). Thus, build-up and high concentration of natural enemies in the field during early season would give the predators a head start to predate on later arriving pests (Costamagna et al., 2015; Settle et al., 1996). Simultaneous assessment of emergent and colonising communities of predators could further elucidate the link between pest control and predator community build- up within fields under agricultural diversification.

Additionally, the reduced disturbance supports species rich and diverse arthropod communities (Tamburini et al., 2016; Tooker et al., 2020), explaining the positive effects of diversification with perennial leys in combination with organic fertiliser on predator richness of all groups in our study. In addition, other habitat dimensions such as soil moisture were highest under combined organic fertilisation and inclusion of perennial leys in the crop rotation (Figure A.2.2) potentially contributing to enhanced overwintering success. Sustaining abundant and rich communities increases community resilience under continuous disturbance from cropping. More diverse predator communities exploit a greater variety of resources (Byrnes et al., 2014), and biodiversity associated to agroecosystems can aid ecosystem functioning such as biological weed and pest control (Soliveres et al., 2016), allowing the coexistence of abundant service providing aboveground predator communities.

Further, disturbance from cropping practices is understood to reduce diversity of soil food webs and results in communities consisting of smaller bodied organisms (Tsiafouli et al., 2015). This could have implications for bottom-up regulation of aboveground predators by soil mesofauna, whereby smaller bodied prey do not provide enough food resources to sustain aboveground predator populations. We did not test for differences in body size in the soil fauna communities, but suggest that the belowground food web probably benefits from lower disturbance and organic subsidies which is likely to strengthen top- down regulation of herbivores (Zelnik et al., 2022).

4.3. Conclusion

We investigated the effect of combined diversification on arthropod communities below and aboveground in crop fields. We conclude that adding organic materials in combination with perennial ley in the crop rotation enhances soil mesofauna abundances and subsequently benefits aboveground predators, in particular staphylinids. While highly abundant soil mesofauna could have sustained predator communities in diversified fields, high weed seed availability could have sustained predators in non-diversified fields leading to less clear differences in predator communities as expected. However, our results highlight that careful assessment of different available prey in the fields is crucial in understanding predator responses to management practices. A more highly replicated study to ascertain statistically significant effect differences, in which feeding links in the food web are also explicitly assessed, e.g., via molecular gut content analysis (e.g. Krey et al., 2021; Roubinet et al., 2017), would clarify these relations.

Lower disturbance in highly diversified fields through extended crop rotations with perennial ley, could have benefits for the overwintering success of predators. It is, hence, possible that pest suppression in fields with low diversification are more dependent on attracting predators from the surrounding landscape. Adopting cropping practices that combine organic fertilisation with extended crop rotations that include perennial leys holds potential to foster biodiversity and increase resilience of communities and ecosystem functions below- and aboveground.

CRediT authorship contribution statement

J.H, M.E.S, R.B conceived the ideas. J.H, M.E.S, R.B, A.T designed the methodology; J.H and M.E.S collected the data; J.H analysed the data and led the writing of the manuscript. R.B & M.E.S supervised the manuscript preparation. All authors contributed to the drafts and gave approval of the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108461.

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Appendix:

Combining organic fertilisation and perennial crops in the rotation enhances arthropod communities

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A.1 Landscape analysis, site selection and experimental set up

We analysed the proportion of arable land and forest cover within a 500 m buffer zone around the field sites. There were no differences in percentage of arable land cover (Anova: χ^{2}=1.340, df=2, p=0.511) or forest cover (Anova:χ^{2}=0.236, df=2, p=0.884) among treatments. Fields were distributed along the Coast of Halland County in southwestern Sweden (Figure A.1).

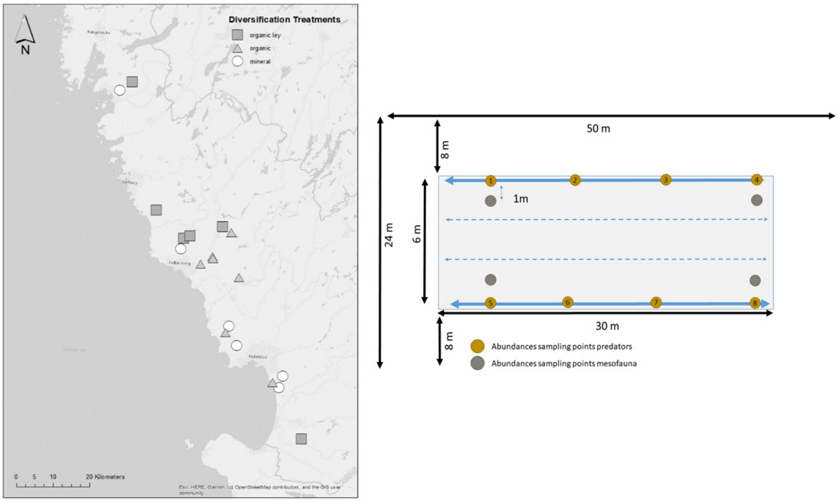


Figure A.1 Locations of 19 spring cereal fields in 2020 in Halland, Sweden (left panel) and experimental set up of the sampling area (right panel). Circular icon represents fields treated with mineral fertiliser, triangular icon represents fields treated only with organic fertiliser and rectangular icon represents fields treated with organic fertiliser and ley in their crop rotation. Total abundance sampling points for aboveground predator communities represented by brown circles, total abundance sampling points for mesofauna samples represented by grey circles.

Table A.1 *Information on field sites 1 to 19 with information on transect placement (B=border, I=Inside field) previous crops in rotation (2014-2020), fertiliser type, soil texture (proportion of clay, silt and sand), soil pH, and the proportion of arable land and forest within a 500m radius from the sampling site.*

Treatment	Field ID	Transect	Crop 2020	Crop 2019	Crop 2018	Crop 2017	Crop 2016	Crop 2015	Crop 2014	Fertiliser type	pH	Clay-%	Silt-%	Sand-%	%-Foest_500m	%-Arable_500m
FminRa	2	B	barley	barley	barley	barley	oat	oat	winter wheat	mineral	6,3	20	30	47	19	68
	9	I	barley	winter wheat	oil seed rape	barley	winter wheat	oat	barley	mineral	6,3	10	22	64	0	96
	13	I	barley	sugar beet	winter wheat	winter wheat	oat	barley	winter wheat	mineral	7,1	6	30	58	8	88
	16	I	barley	barley	oats	barley	oats	oil seed rape	ley	mineral	6,5	18	44	32	10	83
	17	B	oat	barley	barley	barley	winter wheat	barley	winter wheat	mineral	6	< 4	16	78	0	83
	19	B	oat	winter wheat	winter wheat	winter wheat	fava bean	winter wheat	winter wheat	mineral	6,9	16	32	49	0	69
ForgRa	6	I	barley	winter wheat	potato	winter wheat	oil seed rape	pea	barley	liquid manure	6,1	10	30	55	14	63
	7	B	barley	barley	barley	winter wheat	oil seed rape	pea	barley	liquid manure	6,2	12	30	54	0	93
	8	B	barley	barley	winter wheat	winter wheat	oil seed rape	winter barley	winter wheat	manure	5,8	16	47	33	3	85
	10	I	barley	winter wheat	fava bean	barley	winter wheat	oat	barley	liquid manure	6,3	< 4	31	60	19	73
	12	B	barley	barley	kale	winter wheat	potato	barley	pea	manure	5,9	6	17	72	0	91
	15	B	barley	rye	barley	trirticale	oil seed rape	pea	barley	manure	6,4	7	20	69	0	77
	18	I	barley	rye	barley	winter wheat	potato	winter wheat	pea	manure	5,3	< 4	18	75	3	76
ForgRl	1	B	barley	oil seed rape	spring wheat	spring wheat	ley	ley	ley	manure	5,5	7	47	42	30	52
	3	B	oat	barley	rape	ley	ley	ley	barley	manure	5,4	< 4	14	79	1	88
	4	I	barley	spring wheat	ley	ley	ley	spring wheat	barley	liquid manure	5,6	11	31	52	0	97
	5	I	barley	spring wheat	ley	ley	ley	spring wheat	barley	liquid manure	5,6	< 4	22	69	1	86
	11	I	barley	barley	winter wheat	oil seed rape	ley	ley	ley	liquid manure	5,9	< 4	24	63	2	90
	14	B	barley	winter wheat	winter wheat	ley	ley	ley	ley	liquid manure	6,3	6	30	56	0	95

A.2 Soil analysis

Figure A.2.1 (a) Soil organic matter (SOM) content , (b) total nitrogen content and (c) total carbon content in the soil of each diversification treatment: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green).

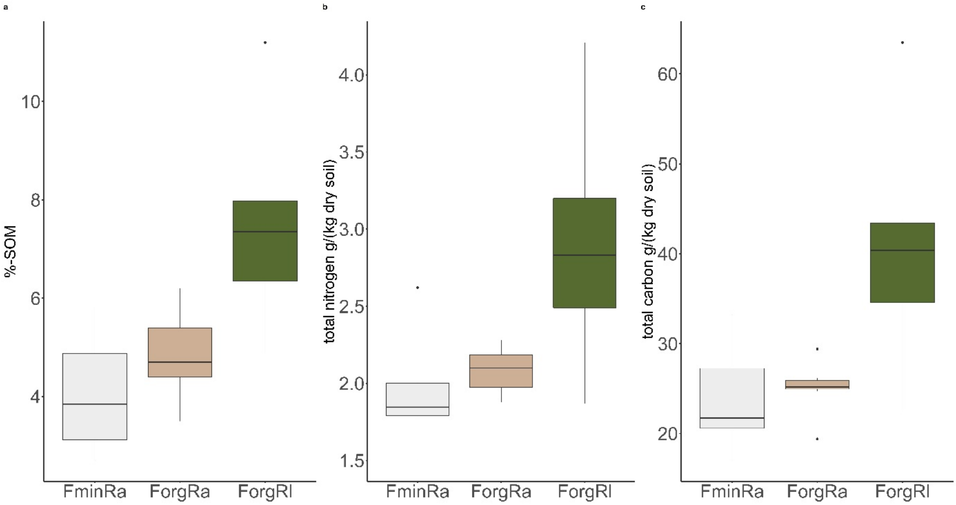


Table A.2.1 *Test statistics with estimates and their standard errors (SE), t-ratios and p-values for pairwise comparisons of treatment effects on %-SOM, nitrogen- and carbon-content in g/kg dry soil. Statistically significant (p<0.05) results are in bold and trends (0.05<p>0.1) are in italic. The intercept is set at fields receiving only mineral fertiliser (no diversification).*

		Estimate	SE	t-value	Pr(>|t|)
SOM	Intercept	4.050	0.609	6.646	<0.005
	ForgRa	0.807	0.830	0.972	0.345
	ForgRl	3.450	0.861	4.003	**0.001**
Nitrogen	Intercept	1.940	0.205	9.457	<0.005
	ForgRa	0.142	0.279	0.511	0.616
	ForgRl	0.966	0.290	3.332	**0.004**
Carbon	Intercept	23.817	3.469	6.865	<0.005
	ForgRa	1.283	4.728	0.271	0.789
	ForgRl	16.833	4.906	3.431	**0.003**

Figure A.2.2 Soil moisture in percent of dry soil during early, mid and late crop stage in the three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green).

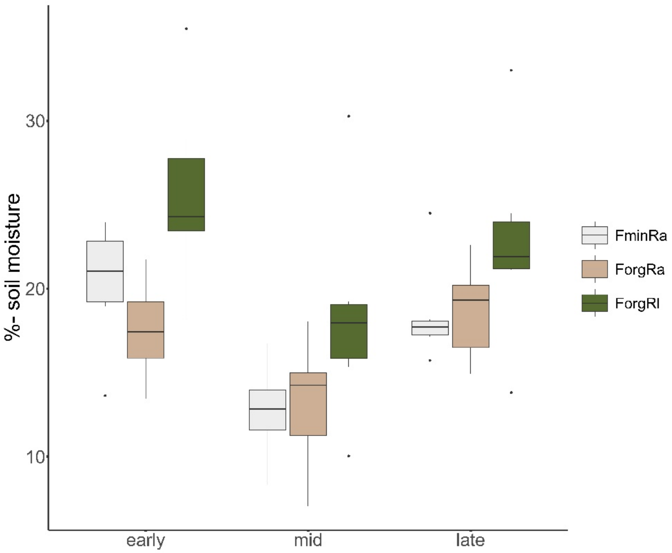


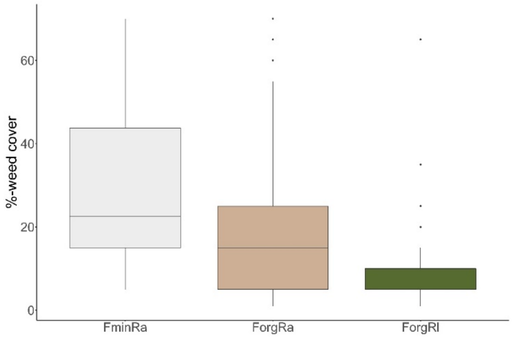
Table A.2.2 *Test statistics with estimates and their standard errors (SE), t-ratios and p-values for pairwise comparisons of treatment effects on soil moisture. Statistically significant (p<0.05) results are in bold and trends (0.05<p>0.1) are in italic. The intercept is set at fields receiving only mineral fertiliser (no diversification).*

	Crop stage	Contrast	Estimate	SE	DF	t.ratio	p-value
Soil moisture	1	FminRa - ForgRa	0.02737	0.0224	46	1.220	0.4475
		FminRa - ForgRl	-0.05438	0.0233	46	-2.337	*0.0607*
		ForgRa - ForgRl	-0.08175	0.0224	46	-3.645	0.0019
	2	FminRa - ForgRa	-0.00410	0.0224	46	-0.183	0.9818
		FminRa - ForgRl	-0.05754	0.0233	46	-2.472	0.0445
		ForgRa - ForgRl	-0.05344	0.0224	46	-2.383	*0.0547*
	3	FminRa - ForgRa	-0.00121	0.0224	46	-0.054	0.9984
		FminRa - ForgRl	-0.04214	0.0233	46	-1.810	0.1775
		ForgRa - ForgRl	-0.04092	0.0224	46	-1.825	0.1729

A.3 Weed cover

We measured weed cover once, during late cropping season as the percentage of ground covered by weeds. We took five sub-measurements and assessed weed cover within a 1m^2 area. Measurements were taken at random locations within the fields to control for patchiness of weed abundances.

Figure A.3 Weed cover in percent area for the three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green).



There was a marginal treatment effect on weed cover (Anova: χ 2=4.596, df= 2, p=0.10, Figure A.3). Fields receiving mineral fertiliser with annual crop rotation had higher weed cover compared to fields receiving the combination of organic fertiliser and perennial leys in the crop rotation (p=0.044).

A.4 Herbivores

Figure A.4.1. Total abundance for the three aboveground arthropod prey groups: (a) flies, (b) small herbivores and (c) large herbivores during mid and late crop stage for the three treatments: mineral fertiliser with annual crops in rotation (FminRa, grey), organic fertiliser with annual crops in rotation (ForgRa, orange) and organic fertiliser with perennial ley in the rotation (ForgRl, green).

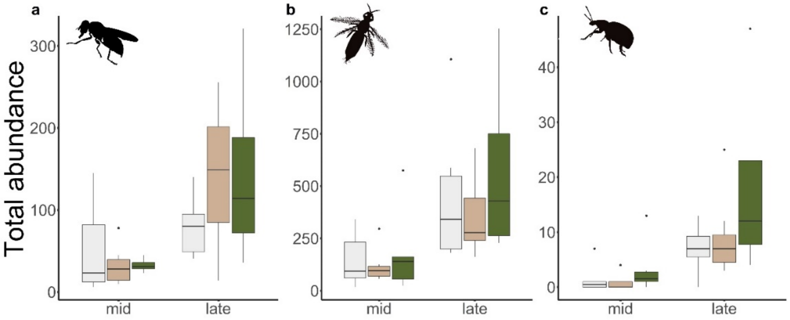


Table A.4. *Test statistics with χ 2-value, degrees of freedom, p-value, marginal and conditional R2 for each model tests on the effects of treatment and crop stage on the total abundance of the three aboveground arthropod prey groups: flies, small- and big herbivores. Statistically significant (p<0.05) results are in bold, trends in italic (0.05<p>0.1). The model on small herbivores was fitted without field identity as a random effect and thus only marginal R2 is presented.*

	Response variable	Explanatory variable	χ^2	DF	p-value	R_m^2	R_c^2
Flies	Total abundance	Treatment	0.084	2	0.9585	0.428	0.558
		Crop stage	24.883	1	<0.005		
Small herbivores	Total abundance	Treatment	2.4965	2	0.287	0.337	
		Crop stage	23.268	1	<0.005		
Big herbivores	Total abundance	Treatment	3.087	2	0.2135	0.586	0.723
		Crop stage	35.453	1	<0.005		

A.5 Pairwise comparisons

Table A.5.1. *Test statistics with estimates and their standard errors (SE), t-ratios and p-values for pairwise comparisons of treatments and crop stage without interactions. Statistically significant (p<0.05) results are in bold and trends (0.05<p>0.1) are in italic. The intercept is set at fields receiving only mineral fertiliser (no diversification). Mineral fertiliser with annual crops in rotation (FminRa), organic fertiliser with annual crops in rotation (ForgRa) and organic fertiliser with perennial ley in the rotation (ForgRl)*

Species	Metric	Contrast	Estimate	SE	DF	t.ratio	p-value
Acari juvenile	Total abundance	FminRa-ForgRa	-0.841	0.354	50	-2.373	*0.0551*
		FminRa-ForgRl	-1.389	0.369	50	-3.761	**0.0013**
		ForgRa-ForgRl	-0.548	0.354	50	-1.547	0.2782
		Sampling1-sampling2	-2.738	0.206	50	-13.299	**<.0001**
		Sampling1-sampling3	-2.534	0.207	50	-12.250	**<.0001**
		Sampling2-samping3	0.204	0.189	50	1.080	0.5305
Mesostigmata	Total abundance	FminRa-ForgRa	-1.28	0.549	50	-2.338	*0.0597*
		FminRa-ForgRl	-1.66	0.563	50	-2.954	0.0130
		ForgRa-ForgRl	-0.38	0.503	50	-0.755	0.7321
		Sampling1-sampling2	-1.790	0.309	50	-5.790	**<.0001**
		Sampling1-sampling3	-1.200	0.318	50	-3.777	**0.0012**
		Sampling2-samping3	0.591	0.249	50	2.370	*0.0555*
Other arthropods	Total abundance	FminRa-ForgRa	-0.533	0.396	50	-1.348	0.3758
		FminRa-ForgRl	-0.788	0.398	50	-1.977	0.1284
		ForgRa-ForgRl	-0.254	0.380	50	-0.670	0.7819
		Sampling1-sampling2	-0.863	0.328	50	-2.635	**0.0296**
		Sampling1-sampling3	-0.671	0.333	50	-2.014	0.1194
		Sampling2-samping3	0.193	0.299	50	0.644	0.7966
Carabid	Total abundance	FminRa-ForgRa	0.452	0.308	50	1.466	0.3159
		FminRa-ForgRl	-0.282	0.319	50	-0.882	0.6538
		ForgRa-ForgRl	-0.733	0.307	50	-2.386	*0.0536*
		Sampling1-sampling2	-0.0735	0.156	50	-0.471	0.8852
		Sampling1-sampling3	-0.4713	0.161	50	-2.935	**0.0137**
		Sampling2-samping3	-0.3977	0.158	50	-2.520	**0.0391**
Carabid	Species richness	FminRa-ForgRa	1.01	1.32	50	0.763	0.7270
		FminRa-ForgRl	-3.17	1.37	50	-2.311	*0.0634*
		ForgRa-ForgRl	-4.17	1.32	50	-3.162	**0.0074**

Species	Metric	Contrast	Estimate	SE	DF	t.ratio	p-value
		Sampling1-sampling2	-1.00	0.764	50	-1.308	0.3974
		Sampling1-sampling3	-2.37	0.764	50	-3.098	**0.0088**
		Sampling2-samping3	-1.37	0.764	50	-1.790	0.1833
Staphylinid	Genus richness	FminRa-ForgRa	-0.556	0.720	50	-0.772	0.7218
		FminRa-ForgRl	-1.944	0.747	50	-2.603	0.0319
		ForgRa-ForgRl	-1.389	0.720	50	-1.930	0.1409
		Sampling1-sampling2	1.79	0.543	50	3.293	**0.0051**
		Sampling1-sampling3	3.05	0.543	50	5.618	**<.0001**
		Sampling2-samping3	1.26	0.543	50	2.325	*0.0615*
Carabid	Shannon diversity	FminRa-ForgRa	-0.0875	0.0957	50	-0.915	0.6334
		FminRa-ForgRl	-0.1425	0.0993	50	-1.435	0.3311
		ForgRa-ForgRl	-0.0549	0.0957	50	-0.574	0.8346
		Sampling1-sampling2	0.0799	0.0966	50	0.826	0.6886
		Sampling1-sampling3	-0.1824	0.0966	50	-1.887	0.1530
		Sampling2-samping3	-0.2622	0.0966	50	-2.713	**0.0243**
Staphylinid	Shannon diversity	FminRa-ForgRa	0.0869	0.101	50	0.862	0.6668
		FminRa-ForgRl	-0.1321	0.105	50	-1.261	0.4235
		ForgRa-ForgRl	-0.2190	0.101	50	-2.170	*0.0863*
		Sampling1-sampling2	-0.222	0.0889	50	-2.503	**0.0407**
		Sampling1-sampling3	0.126	0.0889	50	1.418	0.3396
		Sampling2-samping3	0.348	0.0889	50	3.920	**0.0008**

Table A.5.2 *Test statistics with estimates and their standard errors (SE), t-ratios and p-values for pairwise comparisons of treatments and crop stage with significant interactions. Statistically significant (p<0.05) results are in bold and trends (0.05<p>0.1) are in italic. The intercept is set at fields receiving only mineral fertiliser (no diversification). Treatments contrasted are mineral fertiliser with annual crops in rotation (FminRa), organic fertiliser with annual crops in rotation (ForgRa) and organic fertiliser with perennial ley in the rotation (ForgRl)*

Species	Metric	Crop stage	Contrast	Estimate	SE	DF	t.ratio	p-value
Collembola	Total abundance	1	FminRa - ForgRa	-0.304	0.586	46	-0.519	0.862
			FminRa - ForgRl	-1.528	0.601	46	-2.544	0.037
			ForgRa - ForgRl	-1.224	0.573	46	-2.138	*0.093*
		2	FminRa - ForgRa	-1.278	0.560	46	-2.284	*0.068*
			FminRa - ForgRl	-1.158	0.581	46	-1.993	0.125
			ForgRa - ForgRl	0.120	0.555	46	0.217	0.974
		3	FminRa - ForgRa	-1.225	0.554	46	-2.211	*0.079*
			FminRa - ForgRl	-0.801	0.577	46	-1.389	0.355
			ForgRa - ForgRl	0.424	0.553	46	0.766	0.725
Oribatid mites	Total abundance	1	FminRa - ForgRa	-1.203	1.113	46	-1.081	0.530
			FminRa - ForgRl	-3.108	1.064	46	-2.922	0.014
			ForgRa - ForgRl	-1.9056	0.848	46	-2.248	*0.073*
		2	FminRa - ForgRa	-0.208	0.769	46	-0.271	0.960
			FminRa - ForgRl	-0.556	0.791	46	-0.703	0.763

Species	Metric	Crop stage	Contrast	Estimate	SE	DF	t.ratio	p-value
			ForgRa - ForgRl	-0.348	0.760	46	-0.458	0.891
		3	FminRa - ForgRa	0.1116	0.776	46	0.144	0.988
			FminRa - ForgRl	0.0112	0.802	46	0.014	0.999
			ForgRa - ForgRl	-0.100	0.778	46	-0.129	0.990
Staphylinid	Total abundance	1	FminRa - ForgRa	-0.878	0.364	46	-2.413	*0.051*
			FminRa - ForgRl	-1.255	0.377	46	-3.327	0.004
			ForgRa - ForgRl	-0.377	0.361	46	-1.045	0.552
		2	FminRa - ForgRa	0.115	0.369	46	0.311	0.948
			FminRa - ForgRl	-0.422	0.379	46	-1.114	0.510
			ForgRa - ForgRl	-0.537	0.368	46	-1.456	0.321
		3	FminRa - ForgRa	0.128	0.369	46	0.346	0.936
			FminRa - ForgRl	0.321	0.383	46	0.838	0.681
			ForgRa - ForgRl	0.193	0.368	46	0.525	0.859
Spider	Total abundance	1	FminRa - ForgRa	-0.074	0.262	46	-0.284	0.956
			FminRa - ForgRl	-0.221	0.271	46	-0.817	0.694
			ForgRa - ForgRl	-0.147	0.261	46	-0.563	0.840
		2	FminRa - ForgRa	-0.066	0.261	46	-0.256	0.964
			FminRa - ForgRl	-0.529	0.268	46	-1.974	0.130
			ForgRa - ForgRl	-0.463	0.258	46	-1.798	0.181
		3	FminRa - ForgRa	1.008	0.258	46	3.912	<0.005
			FminRa - ForgRl	0.446	0.266	46	1.677	0.225
			ForgRa - ForgRl	-0.562	0.260	46	-2.166	*0.088*
	Species richness	1	FminRa - ForgRa	-2.167	1.57	46	-1.377	0.361
			FminRa - ForgRl	-4.167	1.63	46	-2.552	0.036
			ForgRa - ForgRl	-2.000	1.57	46	-1.271	0.418
		2	FminRa - ForgRa	-0.667	1.57	46	-0.424	0.906
			FminRa - ForgRl	-0.167	1.63	46	-0.102	0.994
			ForgRa - ForgRl	0.500	1.57	46	0.318	0.945
		3	FminRa - ForgRa	2.929	1.57	46	1.862	0.161
			FminRa - ForgRl	2.667	1.63	46	1.634	0.242
			ForgRa - ForgRl	-0.262	1.57	46	-0.166	0.984
Spider	Shannon	1	FminRa - ForgRa	-0.35195	0.183	46	-1.927	0.1427
			FminRa - ForgRl	-0.45161	0.190	46	-2.382	*0.0547*
			ForgRa - ForgRl	-0.09967	0.183	46	-0.546	0.8492
		2	FminRa - ForgRa	-0.07724	0.183	46	-0.423	0.9064
			FminRa - ForgRl	0.45683	0.190	46	2.410	*0.0514*
			ForgRa - ForgRl	0.53407	0.183	46	2.924	0.0145
		3	FminRa - ForgRa	-0.01245	0.183	46	-0.068	0.9974
			FminRa - ForgRl	- 0.02190	0.190	46	-0.116	0.9927
			ForgRa - ForgRl	-0.00945	0.183	46	-0.052	0.9985

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Beneficial arthropods support farming systems that rely less on external inputs. This thesis investigates how agricultural management diversification affects both above- and belowground beneficial arthropods. Using community and food web analysis, I investigated how trophic interactions between above- and belowground groups impact pest regulation. I show that abundant belowground arthropods promote diverse aboveground predator communities, which in turn, increases pest regulation.

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