Biodiversity conservation and ecosystem service promotion are different but compatible objectives:

Relationships between environmental factors and natural enemies and natural pest control

Zulin Mei

Biodiversity conservation and ecosystem service promotion are different but compatible objectives
Zulin Mei
2024

Propositions

1. The core argument of biodiversity conservation is morality rather than utilitarianism.
   (this thesis)

2. Successful conservation strategies balance the needs of all stakeholders rather than focus only on biodiversity.
   (this thesis)

3. The development of advanced statistical methods is the foundation for better understanding complex systems.

4. Compared to pushing the frontiers of science, too little effort has been made to popularize the outcomes of ground-breaking science understandably to the general public.

5. To understand nature, doing fieldwork is more useful than reading scientific papers.

6. Improving production methods rather than persuading consumers to change their lifestyles is a more feasible way to achieve sustainable development.

7. The current method of presenting scientific results in published papers will be replaced by more intuitive ways of presenting like video or virtual reality.

Propositions belonging to the thesis, entitled

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Zulin Mei

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Chapter 1

General introduction

How to meet the rising demand for agricultural products in a sustainable way

The Earth has stepped into a new geological epoch called the Anthropocene in which the appearance of the planet is characterized by human activity (Lewis & Maslin, 2015). During the Anthropocene, the global population has increased markedly and reached a size of 8 billion in 2022 which is about 2.6-fold higher than that in the 1960s (Zeifman et al., 2022). This trend will continue until the middle of the 21st century with the global population finally peaking at 10 billion (Willett et al., 2019). In addition to the global population explosion, diet shifts with more meat and dairy consumption and the need for biofuels have jointly resulted in a rapidly rising demand for agricultural products (Keyzer et al., 2005; Godfray et al., 2010; Tilman et al., 2011). The Food and Agriculture Organization of the United Nations (FAO) predicted that food demand will increase by on average 1.1% every year until 2050 which indicates that approximately 40% more food needs to be produced in 2050 compared to 2020 (Alexandratos & Bruinsma, 2012). This is predicted to be an impossible mission with the current agricultural production methods (Matson et al., 1997). In the past half century, the Green Revolution has improved agricultural productivity and, by and large, allowed us to meet the continuously increasing demand for agricultural products. The Green Revolution includes many practices such as the selection and use of high-yielding crop cultivars (Khush, 2001; Hedden, 2003) and growing these cultivars as monocultures at high densities to facilitate machine operations which significantly promoted production efficiency (Pingali, 2007). In addition, agrochemicals like mineral fertilizers and artificial pesticides were applied at high rates to improve crop growing conditions which enhanced crop yield per unit area (Liu et al., 2015). These practices achieved a 2.5-fold increase in cereal crop yields during the past half century (Tilman et al., 2002). The practices that are at the basis of the Green Revolution, characterized by agricultural expansion and intensification, are still the dominant paradigm to increase agricultural production in the world.

However, multiple negative externalities caused by Green Revolution practices are becoming more evident (Tilman, 1999; Moss, 2008; Norris, 2008). Agricultural expansion has extensively converted land use types and the total area of agricultural land has increased fivefold from 1700 to 2007. Currently farmland covers about 40% of ice-free land on Earth (Foley et al., 2005; Ramankutty et al., 2018). As a consequence, the area of wetlands and forests has shrunk remarkably which resulted in the significant changes in the biogeochemical cycle (Quinton et al., 2010; Laurance et al., 2018). Agricultural intensification has significantly increased the utilized amounts of agrochemicals. For example, synthetic nitrogen and phosphorous fertilizer consumption per unit cropland has increased about eight and three times respectively between 1961 and 2013 (Lu & Tian, 2017). These processes of agricultural expansion and intensification have severely damaged the environment and skewed the climate, as about 12% of anthropogenic greenhouse gas emissions, particularly 84% of total nitrous oxide emission, can be attributed to agricultural production (Netz et al., 2007; Smith et al., 2008).

Among all of these negative externalities of the Green Revolution, biodiversity loss is one of the most noticeable consequences (Foley et al., 2011). Landscapes consisting of mosaics of ecosystem patches and corridors were replaced by highly homogenized monocultured croplands, which resulted in the degradation and destruction of the natural habitats that are necessary to support biodiversity (Tscharntke et al., 2005; Gámez-Virués et al., 2015). Furthermore, the excessive use of agrochemicals has contaminated the air, soil and water which altered abiotic conditions for organisms (Wilson & Tisdell, 2001). Some agrochemicals can even kill organisms directly, for instance, some broad-spectrum insecticides can poison non-target species and the active substances can transfer and accumulate through trophic levels (Naqvi & Vaishnavi, 1993). Globally, the abundance of two-thirds of monitored invertebrates has declined by 45% in the past 40 years (Dirzo et al., 2014), and the Earth is now facing the Sixth Mass Extinction event (Kolbert, 2014; Raven & Wagner, 2021). Since biodiversity underpins the provisioning of many ecosystem services which are essential to agricultural productivity (Hoehn et al., 2008; Cardinale et al., 2012; Dainese et al., 2019), current agricultural production patterns have led to a dilemma between biodiversity conservation and agricultural productivity. The continuously rising demand for agricultural products pushes agriculture to expand and intensify which threatens biodiversity and associated ecosystem services. Meanwhile, the loss of biodiversity and ecosystem services undermines agricultural productivity. In many countries, crop yields per hectare no longer increases which could be seen as a signal of the consequence of this dilemma (Cassman et al., 2010). Therefore, it is necessary to find more sustainable agricultural production methods that can simultaneously conserve biodiversity and maintain agricultural productivity (Tscharntke et al., 2012).

Ecological intensification: reconciling agricultural productivity and biodiversity conservation via ecosystem services

Ecological intensification has been proposed as a paradigm to guide future agricultural production. Its aim is to make more effective use of ecosystem services in agricultural ecosystems by conserving or restoring biodiversity in agricultural landscapes (Bommarco et al., 2013; Tittonell, 2014). Ecosystem services can be classified into four categories: supporting services, regulating services, provisioning services and cultural services (Millennium Ecosystem Assessment, 2005). As an important component of ecosystems, agricultural ecosystems are important provider of aforementioned four different categories of ecosystem services. Agricultural ecosystems provide supporting services (e.g., nutrient cycling service provided by decomposers) and regulating services (e.g., natural pest control and pollination services provided by natural enemies and pollinators respectively) which then contribute to provisioning services (agricultural products like food and fiber) and cultural services (farm tourism) (Millennium Ecosystem Assessment, 2005). Agricultural productivity (the efficiency of provisioning services by the agricultural ecosystem) is therefore moderated by the delivery of supporting and regulating services and is usually limited by the most limiting underpinning supporting or regulating services (Bommarco et al., 2013). With the current agricultural production methods, agricultural productivity often no longer responds to additional artificial inputs, which indicated that some ecosystem services on farmland have become the limiting factor of agricultural productivity (Classen et al., 2014; Fijen et al., 2020). By converting agricultural production methods from depending on conventional intensification to integrating more natural-occurring ecosystem services, ecological intensification can make agricultural production more sustainable.

The practices involved in ecological intensification can be implemented at multiple spatial scales. At the landscape scale, practices may include the creation or restoration of semi-natural habitats, or improving the quality of existing semi-natural habitats by planting wildflowers. At the field scale, practices may include the implementation of cover crops and conservation tillage (Kleijn et al., 2019). These practices are expected to counteract the negative effects of conventional agricultural practices on services-providing species (Bommarco et al., 2013; Kovács-Hostyánszki et al., 2017; Kleijn et al., 2019), and therefore enhance the delivery of ecosystem services (Tschumi et al., 2015; Tamburini et al., 2016; Tschumi et al., 2016a). The improved ecosystem services can replace the conventional agricultural inputs (ecological replacement) thus minimize the negative environmental impacts (Janssen & van Rijn, 2021), or can improve crop yield without extra anthropogenic inputs (ecological enhancement, e.g., Garibaldi et al., 2016). Ecological replacement and ecological enhancement are not mutually exclusive. They can occur in combination, which would then represent a win-win situation for agricultural production and the environment (Bommarco et al., 2013). In addition, when implemented well, these practices can further support the overall biodiversity other than only the ecosystem service providers (Mlambo, 2021).

However, while ecological intensification is widely advocated in academic and policy-making sectors, many of its proposed practices are poorly adopted by farmers (Kleijn et al. 2019). Inconsistent results regarding the benefits of these practices could be one important factor hindering farmers to adopt such practices. Taking natural pest control services as an example, even though there is generally a consensus that more complex agricultural landscapes can promote the diversity of natural enemies (Chaplin-Kramer et al., 2011; Shackelford et al., 2013; Martin et al., 2016; Dainese et al., 2019), recent studies have produced mixed results and found natural pest control services to be positively (Rusch et al., 2016; Dainese et al., 2019; Larsen & Noack, 2021), neutrally (Chaplin-Kramer et al., 2011; Karp et al., 2018; Martin et al., 2019; Zou et al., 2020) or negatively (Martin et al., 2016; Tscharntke et al., 2016) related with landscape complexity. These inconsistent results indicate that we need to have a deeper understanding why this is the case to allow us to formulate clearer recommendations to entice farmers to integrate ecological intensification into farm management.

How natural pest control is shaped

One factor that is limiting agricultural productivity is crop damage caused by pests. Globally, about 18-26% of crop losses can be ascribed to arthropod pests with an estimated economic value of about $470 billion annually (Culliney, 2014). Thus, measures that can suppress pests are of high economic and social importance (Losey & Vaughan, 2006; Culliney, 2014). Conventional agriculture relies heavily on chemical pesticides, as they can effectively and quickly suppress the pests. The global consumption of chemical pesticides increased 15-20 times from 1960 to 2004 (Oerke, 2005). However, the over-use of chemical pesticides in conventional agriculture is problematic. Pesticides are one of the most hazardous agricultural pollutants in the environment and pesticide residues in food can severely threaten human health (Alavanja et al., 2004; Kim et al., 2017; Tang et al., 2021). Furthermore, pesticide application fundamentally jeopardizes the sustainability of agricultural production as non-target organisms are also impaired by pesticides and such negative effects of pesticides on agrobiodiversity can last for decades (Wick & Freier, 2000; Geiger et al., 2010). Because arthropod natural enemies can also be negatively affected by pesticides applications, this can reduce their functioning or force them to escape. This could weaken the capacity of natural enemies for long-term pest suppression which could ultimately result in the resurgence of target pests or outbreaks of secondary pests (Dutcher, 2007; Bommarco et al., 2011; Hill et al., 2017; Janssen & van Rijn, 2021).

A more sustainable solution is to rely on promoting the pest control services provided by arthropods which are naturally occurring on farmland (Bommarco et al., 2013). Natural enemies suppress pests through “top-down” effects by predation or parasitism (Waage & Greathead, 1988). The efficacy of natural pest control is therefore determined by natural enemy community diversity and composition (Crowder et al., 2010; Griffin et al., 2013; Jonsson et al., 2017; Dainese et al., 2019). To better integrate natural pest control in agricultural production, we need to disentangle how natural pest control is shaped and how it depends on the way multiple environmental factors affect the community diversity and composition of natural enemies (Tylianakis & Romo, 2010).

Understanding how natural enemy communities and associated natural pest control service provisioning are affected by the surrounding environment requires a multi-scale perspective (Tscharntke et al. 2005). At the landscape scale, the majority of the species of natural enemies need resources embedded in multiple different landscape elements because most species are highly mobile (Bianchi et al., 2005; Tscharntke et al., 2008; Rusch et al., 2010). For example, in annual crop systems, harvest and tillage operations destroy the shelters in fields which means that most natural enemies rely on less-disturbed semi-natural habitats for overwintering. The pest control effectiveness of the next growing season is then essentially determined by the overwinter survival rate of natural enemies in the semi-natural habitats (Landis et al., 2000). At the local scale, the on-field management practices can directly affect natural pest control effectiveness by influencing the functioning efficiency of important natural enemy species (Zhu et al., 2020), or indirectly affect natural pest control effectiveness by altering community diversity and composition of natural enemies (Crowder et al., 2010; Garratt et al., 2011). Currently, many studies explore how natural enemy diversity and associated provisioning of natural pest control service can be promoted by focusing on a single practice. This can partly explain why these studies often produced inconsistent results about the effectiveness of a single practice in promoting natural enemy diversity and associated provisioning of natural pest control service as unexamined practices may mask the net effects of the focused practice (Garratt et al., 2011; Veres et al., 2013; Tscharntke et al., 2016).

Besides multiple environmental factors, natural enemies generally come from a wide range of different arthropod orders and families (e.g., beetles, wasps, lacewings, hoverflies and spiders). We therefore also need to account for the fact that different species groups of natural enemies differ in life history traits which may cause them to respond differently to the same environmental factor. For instance, the abundance of carabid beetles and spiders were negatively related to fertilizer application but the abundance of staphylinid beetles was positively related to it (Gagic et al., 2017). Moreover, even species within the same taxon but with different ecological traits can display different response patterns. For example, threatened or rare carabid beetle species are generally specialist species and they experienced a much higher extinction risk than the common species which are generally generalist species (Desender et al., 2010). These inconsistent response patterns suggest that only examining the response pattern of one species group cannot represent the response pattern of the entire natural enemy community in the real world which may hamper our understanding of the overall potential for the delivery of natural pest control to contribute to ecological intensification (Tscharntke et al., 2016; Karp et al., 2018). We need to distinguish which species have adapted well and which species are under threat in agricultural landscape to implement more specific conservation practices.

Furthermore, individual pest species have many different species of natural enemies (e.g., specialist and general predators and parasites). More diverse natural enemy communities should thus provide higher levels of services as different species can occupy different ecological niches and complement each other by consuming pests at different places, times or life stages of pests (Snyder, 2019). However, the assumed positive relationship between natural enemy diversity and pest control effectiveness is not undisputed in the real world. A meta-study showed that even though natural enemy diversity indeed mitigates pest damage on crops, the strength of this relationship varied substantially among studies and was often even negative (Letourneau et al., 2009). One reason for the varying effectiveness of higher natural enemy diversity in enhancing pest control could be that the species providing most of the services to farming are different species than the species that are threatened in their existence (Kleijn et al., 2011). The delivery of ecosystem services is generally determined by the abundance of the most dominant species but not by the species richness of threatened species (Kleijn et al., 2015; Winfree et al., 2015). Another reason could be that different species groups could interfere or even predate each other (Finke & Denno, 2005; Straub et al., 2008), and these intraguild interferences or predation can weaken the pest control efficiency of natural enemies and even disrupt natural pest control (Finke & Denno, 2003; Martin et al., 2013).

One important but often overlooked natural enemy community character is natural enemy evenness (Snyder, 2019). Higher natural enemy community evenness can promote the delivery of natural pest control, as higher evenness can guarantee each niche is completely occupied and even mitigate natural enemy intraguild predation (Crowder et al., 2010; Snyder, 2019). However, Hillebrand et al. (2008) argued that the efficiency of ecosystem functioning of a community is determined by the most efficient species, and thus higher evenness may dilute the functioning efficiency. In the real world, studies also produced mixed results of the relationship between natural enemy evenness and pest control effectiveness (Crowder et al., 2010; Rusch et al., 2015; Mace & Mills, 2017; Riggi et al., 2017; Dainese et al., 2019; Yuan et al., 2019). To better exploit natural pest control, we need to improve our understanding of the mechanisms how natural pest control service delivery is affected by natural enemy community composition components other than community abundance and diversity.

Study system and outline of this thesis

The main aim of this thesis is to test the evidence base for how the community diversity and composition of multiple natural enemy species groups are affected by environmental factors at different spatial scales, and how the efficiency of natural pest control delivery is affected by the community evenness and composition of natural enemies. I carried out three empirical across-landscapes studies and one controlled fully experimental study. These studies used wheat (*Triticum aestivum*) as the model system, as wheat is one of the most important and widely cultivated crops all over the world and wheat productivity is key in bolstering global food security (Leff et al., 2004; Curtis & Halford, 2014). In the three landscape-level studies, I selected three ground-dwelling natural enemy guilds as bioindicators: carabid beetles (Carabidae), spiders (Araneae) and staphylinid beetles (Staphylinidae). These guilds represent the three important groups of natural enemies in arable fields and are widely used as bioindicators (Bohac, 1999; Lang et al., 1999; Borchard et al., 2014). In the experiment, I examined the effects of natural enemy evenness on aphid predation by using a model system with the aphid species *Sitobion avenae* on wheat (*Triticum aestivum*), as *S. avenae* is one of the most dominant pests of winter wheat in Europe and its risky area is predicted to be expanded in near future (Vickerman & Wratten, 1979; Wang et al., 2023).

In this thesis, I explored how natural pest control is shaped and delivered hierarchically. In chapter 2, I examined the effectiveness of wildflower strips, an important ecological intensification practice, in promoting natural enemies and how this practice can affect aphid pest suppression efficiency and crop yield. Furthermore, I determined whether the response of natural enemies, aphids and crop yield depends on flower cover and species richness of the wildflower strips, and whether this was moderated by fertilizer and insecticide applications. In chapter 3 and 4, I carried out two multi-country analyses which explored how multiple guilds of natural enemies respond to environmental factors at different spatial scales. Specifically in chapter 3, I used carabid beetles and spiders collected in four countries in north-western Europe and examined how their abundance, species richness and evenness (α-diversity) were jointly affected by crop yield (as a proxy of local land-use intensity), percentage cropland (a proxy for landscape complexity) and soil organic carbon content, and whether these patterns differed between dominant and non-dominant species. In chapter 4, using the same data as chapter 3, I examined how β-diversity of carabid beetles and spiders was affected by distance and the difference between or the mean of the crop yield, the percentage cropland and the soil organic carbon content of pairs of sampling locations. In chapter 5, I explored the underlying mechanisms of how natural enemy evenness and composition affected natural pest control. I carried out a control experiment which exposed *S. avenae* aphid colonies in experimental cages to natural enemy communities that had the same abundance and species richness but that differed in evenness and dominant species. The results of my studies are brought together in chapter 6 where the implications and conclusions of this thesis are discussed and synthesized in the context of the recent developments in this field of research.

Chapter 2

Flower availability drives effects of wildflower strips on ground-dwelling natural enemies and crop yield

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Abstract

Wildflower strips have been heralded as a promising way to enhance ecosystem services by providing organisms which may help make farming less dependent on external inputs. However, recent studies show inconsistent effects on delivery of ecosystem services and crop yield, warranting a more detailed analysis of the factors determining the effects of wildflower strips. We examined how the natural enemy groups of spider, carabid beetle and staphylinid beetle, as well as aphid pest and crop yield respond to wildflower strips. We furthermore determined whether the response of natural enemies, aphids and crop yield depends on flower cover and species richness, and how this is influenced by fertilizer and insecticide applications to the crop in 16 winter wheat fields in the Netherlands. We used an experimental approach with a nested design that included all combinations of wildflower strips (present/absent), fertilizer application (yes/no) and insecticide application (yes/no). Presence of wildflower strips did not affect ground-dwelling natural enemies, aphids or crop yield. However, flower availability across wildflower strips and control margins was positively related to the abundance of the pooled number of examined natural enemies, spiders and carabid beetles. Positive effects in the crop were observed over limited distances; up to 5 m from the edge for spiders and wheat yield. The effects of flower availability and on-field management practices on natural enemies, aphids and wheat yield did not interact suggesting that, in our study, effects of flowers were not influenced by insecticide or fertilizer applications but were mainly additive. Our study indicates that cover and richness of wildflowers in field margin habitat, rather than establishment of wildflower strips per se, drove increases in natural enemies and crop yield. This suggests that more attention should be given to the optimization of establishment success of seed mixtures and management practices enhancing wildflower cover and diversity. Furthermore, biodiversity enhancing management of the herbaceous vegetation in linear landscape elements may represent a cost-effective alternative to boost ecosystem services regulating crop production in agricultural landscapes.

Key words

agricultural production; conservation biological control; ecological intensification; field margin; flower diversity; habitat management; semi-natural habitat

Introduction

Expansion and intensification of agriculture since the Green Revolution in the 1960s have boosted agricultural production, but have had significant negative impacts on the environment (Matson et al., 1997). Conversion of natural ecosystems into farmland and excessive use of agrochemicals have resulted in loss and degradation of habitat and strong declines in farmland biodiversity (Tscharntke et al., 2005; Gámez-Virués et al., 2015). As biodiversity underpins the ecosystem services that are critical for agricultural production, such as pollination, natural pest control and nutrient cycling, long-term agricultural productivity may be jeopardized if current biodiversity declines continue (Tscharntke et al., 2005; Rusch et al., 2013a; Dainese et al., 2019). With the global human population continuously increasing, meeting the growing demands for food in a sustainable way is a serious challenge for mankind in the next decades (Godfray et al., 2010).

Ecological intensification has been proposed as an approach to reduce anthropogenic pressure on the environment while maintaining agricultural productivity (Bommarco et al., 2013). Ecological intensification proposes to replace external inputs with ecosystem services to increase the sustainability of farming. One of the key ecosystem services supporting crop production is natural pest control, with an estimated economic value of $ 4.5 billion per year in the USA alone (Losey & Vaughan, 2006). Delivery of pest control services in agricultural fields has been shown to depend on the composition of the surrounding landscape, with landscapes containing less semi-natural habitats providing less pest control services and lower crop yield (Dainese et al., 2019). This suggests that in simplified agricultural landscapes where few semi-natural habitats remain, creating new semi-natural habitats may be an effective way of enhancing natural pest control (Veres et al., 2013).

In intensively farmed landscapes, field margin habitats such as ditch banks, hedges and roadside verges make up a significant proportion of the semi-natural habitats. Field margins can provide less-disturbed overwintering sites to natural enemies, as well as essential resources when these are unavailable in the crop. The suitability of field margins as habitat for natural enemies can be further enhanced by expanding them and sowing wildflower mixtures, thereby providing pollen and nectar for flower-visiting species groups such as hoverflies and parasitoid wasps (Bianchi & Wäckers, 2008; Haaland et al., 2011). Such wildflower strips may benefit natural enemies that do not or rarely use floral resources, such as spiders, carabid beetles and staphylinid beetles as well because they can provide long-term stable shelters and complex vertical vegetation structures that are important for these organisms (Frank & Reichhart, 2004; Schmidt-Entling & Döbeli, 2009). However, while wildflower strips have generally been shown to benefit natural enemies (Blaauw & Isaacs, 2015; Tschumi et al., 2015), the effects of wildflower strips on ecosystem service delivery are less consistent, with studies showing positive, neutral and even negative effects on natural pest control in nearby crops (Pfiffner et al., 2009; Tscharntke et al., 2016; Tschumi et al., 2016a; Grab et al., 2018; Toivonen et al., 2018; Cahenzli et al., 2019; Albrecht et al., 2020). This makes it difficult to formulate clear recommendations that help entice farmers to integrate wildflower strips into farm management.

One reason for the varying effectiveness of wildflower strips in enhancing pest control could be variation in the quantity and quality of the floral resources they provide (Pollier et al., 2019; Albrecht et al., 2020). Flower abundance and diversity varies markedly between wildflower strips because different seed mixtures are being used (Haaland et al., 2011) or because of variation in establishment success at the species or even whole mixture level (Scheper et al., 2015). Furthermore, the quality of wildflower strips often decreases with time since establishment if management practices are inadequate (De Cauwer et al., 2005), potentially weakening their effectiveness in attracting and preserving natural enemies (Frank et al., 2012). Wildflower strip effectiveness is furthermore determined by the floral diversity of the pre-existing field margins. Sowing wildflowers next to an abundantly flowering margin creates a smaller ecological contrast may therefore result in lower impact than sowing wildflowers next to a field margin devoid of flowers (Kleijn et al., 2011; Scheper et al., 2013). While the diversity of wildflower strips is often considered as a variable explaining the effectiveness of wildflower strips (Scheper et al., 2013; Albrecht et al., 2020), the role of the diversity of the pre-existing field boundary is rarely examined (but see Bischoff et al., 2016; Pollier et al., 2018).

Another reason for the varying effectiveness of wildflower strips could be that the effects of wildflower strips depend on farm management (Sutter et al., 2018). For example, spraying insecticides may not only impact the target pest species but also negatively affect non-target species, such as natural enemies (Bommarco et al., 2011). Harming key predators may reduce effective longer-term suppression of the target pest species which could ultimately increase pest abundance or even result in outbreak of secondary pests (Hill et al., 2017). The use of insecticides may therefore counteract positive effects of establishing semi-natural habitats through unintentional side-effects on natural enemies (Gagic et al., 2019). Fertilizer application may also indirectly influence the effectiveness of wildflower strips through effects on both natural enemies and pests (Garratt et al., 2011). For instance, Garratt et al. (2018) found that the aphid species *Metopolophium dirhodum*, but not *Sitobion avenae*, was more abundant in fertilized than in unfertilized wheat crop plots. Gagic et al. (2017) also found that fertilizer application to wheat crops reduced activity density of wolf spiders but increased activity density of staphylinid beetles. Therefore, the net effects of fertilizer application on natural pest control probably depend on the local context, which is determined by, amongst others, crop, pest species and composition of natural enemy community (Birkhofer et al., 2008). How the effects of on-field management on natural pest control interact with effects of wildflower fields is virtually an unexplored territory.

Here, we examined the effects of wildflower strips on natural pest control and crop yield in winter wheat (Triticum aestivum) fields with contrasting management in the Netherlands. We selected eight fields bordering a 3-5 m wide wildflower strip on one side and eight fields without wildflower strips as control. Each field was subdivided into four plots that were subject to all combinations of fertilizer application (with, without) and insecticide application (with, without). We subsequently quantified the abundance of the total and most dominant groups of natural enemies and aphids, as well as crop yield and examined how this was influenced by presence and quality of wildflower strips and on-field management. We specifically asked (1) whether effects of wildflower strips on natural enemies, aphids and crop yield are affected by wildflower cover and diversity and (2) whether and how effects of wildflower strips on natural enemies, aphids and crop yield are influenced by insecticide and fertilizer applications.

Material and methods

Study system and site selection

The study area, the Flevopolder, is land that was reclaimed in the 1950's and 1960's from a former inner sea in the center of the Netherlands. Most of the land was shaped into a mosaic of square agricultural fields separated by roads and drainage ditches, although small forest areas were planted scattered throughout the area (Fig. 2.1). Soils mostly consist of sea clay and thus typically are mineral-rich, fine-textured and mostly low in percentage of organic material. Most farmers use a crop rotation scheme that includes potato, onion and wheat. In the study year 2014, about 20% of the total agricultural area in this region consisted of winter wheat (CBS, 2015).

We selected sixteen winter wheat fields (Fig. 2.1), all of which were located on clayey soils. At eight sites, a mixture of perennial flowering plant species had been sown in 2-4 m wide strips to replace the pre-existing field boundaries of the wheat fields. These wildflower strips had been sown at least one year prior to the experiment. The exact composition of the flower mixture varied between strips, but typically included *Trifolium repens*, *Lotus corniculatus*, *Cichorium intybus*, *Medicago sativa*, *Achillea millefolium* and *Leucanthemum vulgare*. The other eight wheat fields served as control sites and were bordered by a standard field boundary, which had similar characteristics as the pre-existing field boundaries where the wildflower strips had been sown: a width of about 2 m and usually a ditch bank, and vegetation dominated by coarse grass species. The average closest distance between experimental wheat field sites was 12.2 km (range from 0.35 to 36.4 km).

Experimental setup per site

In each wheat field we established an experimental site of 80 x 25 m, with the longer side adjacent to the wildflower strip or control field margin. Farmers were asked to avoid the application of organic or mineral fertilizer and the spraying of insecticides in this area, while otherwise maintaining all regular management practices. To assess the impact of fertilizer and insecticide application, each site was subdivided into four plots (20 x 25 m each), and all combinations of fertilizer application (with, without) and insecticide application (with, without) were randomly assigned to four plots (Fig. S2.1a). The nitrogen fertilizer (two gifts of calcium ammonium nitrate) was applied in mid-March and early April, containing 80 and 90 kg N per hectare respectively. The insecticide (Karate Zeon® Syngenta, Bergen op Zoom, the Netherlands, main active ingredient lambda-cyhalothrin w/w=2.5%-10%) was sprayed in May at the heading stage of the wheat (BBCH 50; Zadoks et al., 1974) with a dosage of 50 mL/ha.

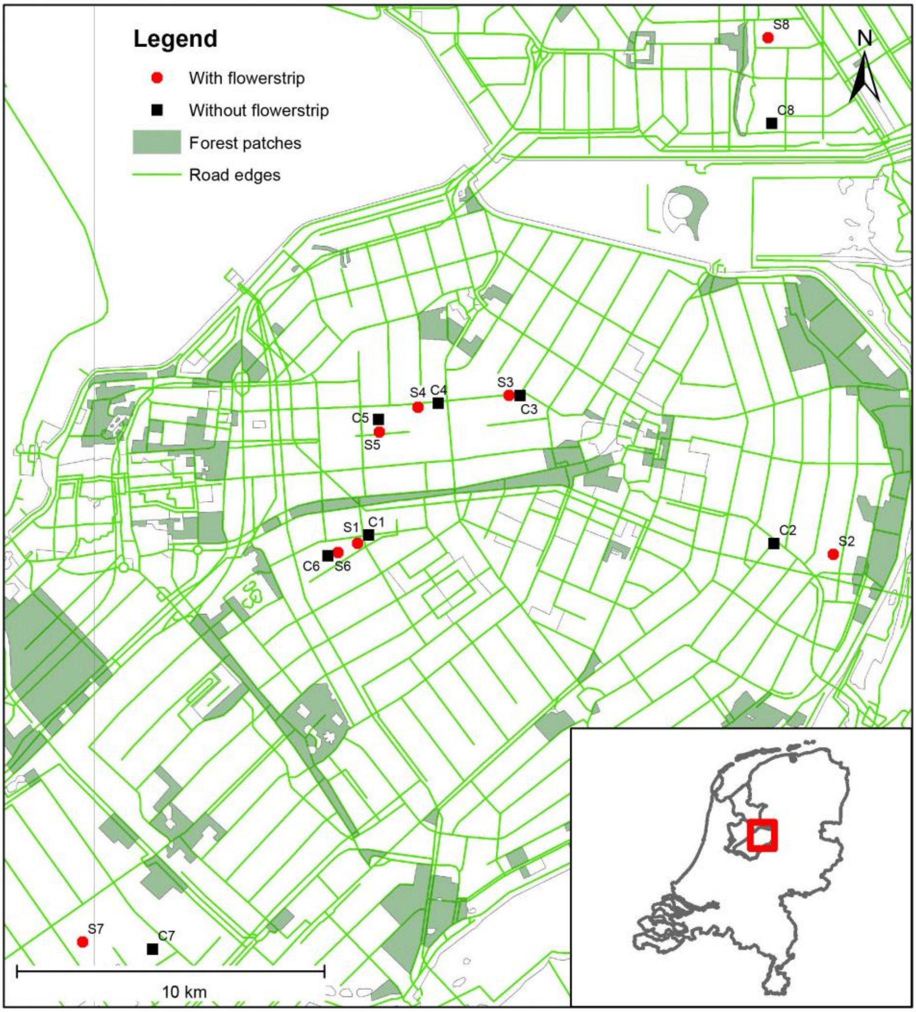

Fig. 2.1. Geographical map of the study area, showing the locations of the 16 study sites. C represents control sites without wildflower strips; S represents sites sown with wildflower strips.

Flower characterization and pest and natural enemy surveys

Flower cover and species richness were assessed on 7 and 8 July 2014 in the pre-existing boundaries of the control sites and in the wildflower strips, just after the last survey round of pest and natural enemies had finished (see below) during the peak of floral resource availability. Flowering species were recorded in a 25 meter transect by laying down a line and recording all species that had open flowers directly next to both sides of this line. Flower cover was assessed in three 1 m^2 plots per transect (on both ends and in the middle of the line) by visually estimating (from directly above the plot) the percent of ground area covered by open flower heads (Fig. S2.1a). Flower cover values were averaged per plot. All flower observations were done by the same person.

Per plot, abundance of pests (*Sitobion avenae*) and ground-dwelling predator were assessed during three inventory rounds, in April (stem elongation stage; BBCH 35), May (heading stage; BBCH 50) and June (flowering stage; BBCH 60). Inventories were conducted within field margins (wildflower strips and control; 0 m from field margin) and in the crop at distances of 5, 10 and 20 m from the field margin. The number of live aphids were counted on 17 wheat tillers in each of two transects per distance, with parallel alignment to the field margin ($17\times2\times3=102$ tillers inspected per plot). Ground-dwelling natural enemies were captured by pitfall traps (plastic beer cups, height 154.5 mm and diameter 95 mm), with four pitfall traps per plot: one within the field margin and three in the crop at distances of 5, 10 and 20 meters (Fig. S2.1b). Each pitfall trap was filled with 200 mL of a mixture of 2/3 water and 1/3 glycol. After 5 days, pitfall traps were emptied and arthropods were collected and stored in 70% ethanol solution to be furthered classified. Specimens were subsequently sorted and counted and, for the purpose of this study, the number of individuals of the three most abundant groups of natural enemies was determined: Aranae (spider), Carabidae (carabid beetle) and Staphylinidae (staphylinid beetle).

Wheat yield measurements

Ripe wheat ears were manually harvested in all plots, within days before the whole field was harvested (late July 2014). Per plot, we harvested in total 1 m^2 at 5, 10 and 20 m distance from the field margin respectively, by placing four subplots of 0.25 m^2 along a line parallel to the margin at each distance (Fig. S2.1b). Harvested ears were transported in cotton bags and dried by hanging the open bags in a climate room with constant temperature of 25 °C and air humidity of 10%. After threshing, we measured the total fresh weight per replicate batch and the fresh and dry weight of a ~50-gram subsample, in order to calculate total grain yield in gram/m^2 (standardized to a moisture content of 14%).

Analysis

We excluded the unfertilized treatment plots from three fields (two wildflower strip sites, one control site) from the analyses as it turned out that the respective owners of the fields had accidentally fertilized these plots. As a result, we ended up with a total of 48 experimental plots, with 232 sampling points for the natural enemies (including those in the wildflower strip and control field margin) and 174 sampling points for the aphids and wheat yield.

Abundance data of ground-dwelling natural enemy (spider, carabid beetle and staphylinid beetle) and aphid were pooled over rounds per sampling point, and were ln (x + 1) transformed to improve normality and homoscedasticity of residuals.

The focus of our analyses was to experimentally test the effects of wildflower strips and on-field management on natural enemies, pests and crop yield. However, because the abundance of natural enemies and pests may be affected by landscape context, we first explored whether these were related to the proportion semi-natural habitat (forests, heathlands, orchards, roadside verges, dikes and hedgerows) in a 500 m radius around our experimental plots using linear mixed effects models with semi-natural habitat cover as fixed effect and field ID, with fertilizer and insecticide treatments nested in field ID, as random effects to correct for the multiple samples from the same site. Semi-natural habitat cover ranged from 1.1% to 26.5% (mean ± SD: 11.1% ± 8.2%) and was not significantly related to spiders ($\chi^2_{(1)}$ =1.17, P = 0.28), carabid beetles ($\chi^2_{(1)}$ =0.09, P = 0.77), staphylinid beetles ($\chi^2_{(1)}$ =1.64, P = 0.20) or aphids ($\chi^2_{(1)}$ =0.50, P = 0.48). We subsequently did not consider landscape context in the main analyses of our study.

Welch's t-test was used to compare flower cover and species richness between wildflower strips and control margins. We used linear mixed effects models and an information theoretic approach to analyze effects of wildflower strips and on-field management on abundance of natural enemies. Analyses were performed for each of the main natural enemy species groups separately: spider, carabid beetle and staphylinid beetle and total natural enemy. We constructed a global model that included wildflower strip treatment (yes/no), fertilizer application (yes/no), insecticide application (yes/no), distance from the field boundary (0, 5, 10, 20 m) and all their two-way interactions as fixed effects, and field ID, with fertilizer and insecticide treatments nested in field ID, as random effects. Next, we used the global model to construct an all-subsets model set consisting of all possible combinations of the fixed factors and their two-way interactions. We restricted our analyses to two-way interactions to limit model complexity and the total number of models considered, given the sample size (Burnham et al., 2011). To examine effects of floral quality of wildflower strips and control field margins, we furthermore added models in which we replaced the binary wildflower strip treatment variable with the continuous variables flower species richness and flower cover. Comparisons of the performance of model sets therefore included models with either presence of wildflower strips (yes/no) or, regardless of field margin type, flower cover or flower species richness of field margins. Flower cover was ln (x + 1) transformed to reduce positive skew. A similar approach was used to examine effects on aphid abundance and crop yield, with the exception that these analyses only concerned within-field data and distance from field boundary therefore only included data collected at 5, 10 and 20 m from field margins.

Models were ranked based on their Akaike Information Criterion values corrected for small sample size (AICc) and we restricted our candidate set to models with Δ AICc < 2 (Burnham et al., 2011). Akaike model weights (ω), which reflects the probability that a model is the best approximating model in the candidate set, were calculated for each model in the candidate set. In the interest of parsimony, in case models in a candidate set included more complex versions of a model with a lower AIC value, we based our inference on this simpler model (Richards, 2008; Richards et al., 2011). To aid interpretation of effects we present significance tests for parameter estimates in Table S2.1. All analyses were performed using R version 3.5.0 (R Core Team 2018).

Results

Trifolium sp., *Lotus corniculatus*, *Taraxacum officinale* and *Plantago lanceolata* were dominant species and presented in majority of wildflower strips. Floral quality varied a lot between different strips, with flower cover and species richness ranging from 1% to 55% and 3 to 11 respectively in the sown strips and ranging from 0 to 1% and 0 to 4 respectively in the control strips. Nevertheless, both flower cover ($t_{8.09} = -3.305$, $P = 0.011$) and species richness ($t_{9.60} = -4.2994$, $P = 0.002$) of wildflower strips were significantly higher than those of control sites. Flower cover and flower richness were significantly correlated across all sites ($r = 0.598$, $P = 0.014$).

Natural enemies

In total, 10,150 individuals of ground-dwelling natural enemies were captured during the experiment with 1,349 spiders, 4,423 carabid beetles, 4,246 staphylinid beetles and 132 arthropods of other taxa. All natural enemies were captured in May and June; in April no natural enemies were captured at all. Presence of wildflower strips did not feature in any of the best models explaining abundance of any of the natural enemy groups (Table 2.1a, b). Flower cover and species richness on the other hand featured prominently, albeit in interaction with other factors, in the models that best explained abundance of total natural enemies, spiders and carabid beetles. Abundance of total natural enemies was best explained by a model including distance to field margins, flower cover and the interaction between the

Table 2.1. Candidate models (Δ AICc < 2) explaining the change in abundance of natural enemies (a, b, c and d) and aphids (e) and yield of winter wheat (f). AICc values of null models (intercept-only) are added for reference. Models are ranked in order of increasing differences in corrected Akaike Information Criterion (ΔAICc), Akaike model weights (ω) indicate the probability that a model is the best approximating model in the candidate set. Dx, distance from field margins (5 m, 10 m and 20m); F, fertilizer application (yes/no); I, insecticide application (yes/no); WFS, treatment (wildflower strips/control sites); FC, flower cover; FR, flower species richness. Variables WFS, FC and FR were never included together in the same model.

(a) Total natural enemies

Explanatory variable	Model set								Null model
	1	2	3	4	5	6	7	8	
D_5	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	
D_{10}	0.19	0.19	0.19	0.19	0.19	0.19	0.19	0.19	
D_{20}	0.25	0.25	0.25	0.25	0.25	0.25	0.25	0.25	
F		0.10	0.10	0.10			0.10	0.10	
I			0.11	0.11	0.11	0.11		0.11	
WFS									
FC	0.64	0.63	0.63	0.63	0.64	0.65	0.64	0.64	
FR									
$FC\times D_5$	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	-0.70	
$FC\times D_{10}$	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	-0.54	
$FC\times D_{20}$	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	
FC×F		-0.35	-0.34	-0.34					
FC×I				-0.27		-0.27			
$FR\times D_5$									
$FR\times D_{10}$									
$FR\times D_{20}$									
FR×F									
FR×I									
$F\times D_5$									
$F\times D_{10}$									
$F\times D_{20}$									
$I\times D_5$									
$I\times D_{10}$									
$I\times D_{20}$									
F×I									
d.f.	11	13	14	15	12	13	12	13	4
AICc	451.0	451.1	451.9	451.9	451.9	452.1	452.2	453.0	464.9
ΔAICc	0	0.07	0.86	0.87	0.89	1.10	1.12	1.99	13.9
ω	0.184	0.178	0.120	0.119	0.118	0.106	0.106	0.068	<0.001

(b) Spiders

Explanatory variable	Model set						Null model
	1	2	3	4	5	6	
D_5	-0.24	-0.24	-0.24	-0.24	-0.24	-0.24	
D_{10}	-0.53	-0.53	-0.53	-0.53	-0.53	-0.53	
D_{20}	-0.42	-0.42	-0.42	-0.42	-0.42	-0.42	
F	-0.31	-0.31	-0.31	-0.31	-0.31	-0.31	
I	0.03	-0.36	0.03	0.03	0.03	-0.36	

Continued Table 2.1(b)

Explanatory variable	Model set 1	2	3	4	5	6	Null model
WFS							
FC	0.85	0.85	0.85	0.85	0.85	0.85	
FR							
FC×D_5	-0.39	-0.39	-0.39	-0.39	-0.39	-0.39	
FC×D_{10}	-0.81	-0.81	-0.81	-0.81	-0.81	-0.81	
FC×D_{20}	-0.92	-0.92	-0.92	-0.92	-0.92	-0.92	
FC×F			-0.24			-0.24	
FC×I				-0.22			
FR×D_5							
FR×D_{10}							
FR×D_{20}							
FR×F							
FR×I							
F×D_5							
F×D_{10}							
F×D_{20}							
I×D_5	-0.49		-0.49	-0.49	-0.49		
I×D_{10}	-0.49		-0.49	-0.49	-0.49		
I×D_{20}	-0.56		-0.56	-0.56	-0.56		
F×I					-0.15		
d.f.	16	13	17	17	17	14	4
AICc	495.4	496.3	496.4	496.6	497.2	497.3	538.4
ΔAICc	0	0.95	1.06	1.23	1.84	1.94	43
ω	0.283	0.176	0.167	0.153	0.113	0.107	<0.001

(c) Carabid beetles

Explanatory variable	Model set 1	2	3	4	5	6	7	Null model
D_5	0.05	0.05	0.05	0.05	0.05	0.05	0.05	
D_{10}	0.36	0.36	0.36	0.36	0.36	0.36	0.36	
D_{20}	0.41	0.41	0.41	0.41	0.41	0.41	0.41	
F	-0.46	-0.44	-0.19	-0.46	-0.19	-0.44	-0.46	
I		0.20			0.20		0.20	
WFS								
FC				0.49			0.49	
FR	0.44	0.44	0.44		0.44	0.44		
FC×D_5				-0.82			-0.82	
FC×D_{10}				-0.48			-0.48	
FC×D_{20}				-0.70			-0.70	
FC×F				-0.68			-0.68	
FC×I								
FR×D_5	-0.98	-0.98	-0.98		-0.98	-0.98		
FR×D_{10}	-0.73	-0.73	-0.73		-0.73	-0.73		
FR×D_{20}	-0.68	-0.68	-0.68		-0.68	-0.68		
FR×F						-0.23		
FR×I								

Continued Table 2.1(c)

Explanatory variable	Model set							Null model
	1	2	3	4	5	6	7	
F×D_5			-0.05		-0.05			
F×D_{10}			-0.40		-0.40			
F×D_{20}			-0.56		-0.56			
I×D_5								
I×D_{10}								
I×D_{20}								
F×I								
d.f.	12	13	15	13	16	13	14	4
AICc	618.1	618.8	618.9	619.5	619.6	619.9	620	635.2
ΔAICc	0	0.62	0.73	1.4	1.42	1.75	1.9	17.1
ω	0.236	0.173	0.164	0.118	0.116	0.098	0.095	<0.001

(d) Staphylinid beetles

Explanatory variable	Model set							Null model
	1	2	3	4	5	6	7	
D_5								
D_{10}								
D_{20}								
F	0.75	0.75	0.75	0.75	0.75	0.75	0.75	
I			0.09	0.09	0.09			
WFS							-0.08	
FC								
FR		-0.21		-0.21	-0.21	-0.22		
FC×D_5								
FC×D_{10}								
FC×D_{20}								
FC×F								
FC×I								
FR×D_5								
FR×D_{10}								
FR×D_{20}								
FR×F						-0.17		
FR×I				-0.30				
F×D_5								
F×D_{10}								
F×D_{20}								
I×D_5								
I×D_{10}								
I×D_{20}								
F×I								
d.f.	5	6	6	8	7	7	6	4
AICc	558.8	559.3	560.1	560.5	560.6	560.7	560.7	593.3
ΔAICc	0	0.45	1.3	1.73	1.77	1.89	1.9	34.5
ω	0.254	0.203	0.133	0.107	0.105	0.099	0.098	<0.001

(e) Aphids

Explanatory variable	Model set				Null model
	1	2	3	4	
D_{10}		0.03	0.03		
D_{20}		0.02	0.02		
F					
I	-0.47	-0.47	-0.47	-0.47	
WFS				0.18	
FC		-0.53	-0.53		
FR					
FC×D_{10}		0.73	0.73		
FC×D_{20}		0.75	0.75		
FC×F					
FC×I			0.18		
FR×D_{10}					
FR×D_{20}					
FR×F					
FR×I					
F×D_{10}					
F×D_{20}					
I×D_{10}					
I×D_{20}					
F×I					
d.f.	5	10	11	6	4
AICc	422.1	422.1	423.8	423.8	434.7
ΔAICc	0	0.08	1.72	1.77	12.6
ω	0.357	0.344	0.151	0.148	<0.001

(f) Yield

Explanatory variable	Model set		Null model
	1	2	
D_{10}	86.25	86.25	
D_{20}	103.18	103.18	
F	567.87	573.16	
I			
WFS			
FC			
FR	103.38	103.33	
FC×D_{10}			
FC×D_{20}			
FC×F			
FC×I			
FR×D_{10}	-137.23	-137.51	
FR×D_{20}	-115.80	-115.37	
FR×F			
FR×I			
F×D_{10}		29.42	
F×D_{20}		-45.28	
I×D_{10}			
I×D_{20}			

Continued Table 2.1(f)

Explanatory variable	Model set 1	Model set 2	Null model
F×I			
d.f.	10	12	4
AICc	2239.4	2241	2378.3
ΔAICc	0	1.61	138.9
ω	0.691	0.309	<0.001

two factors (Table 2.1a and S2.1). Although there were seven other candidate models within Δ AICc < 2, these were all more complex versions of the highest-ranking model (Table 2.1a). In the field margins, total natural enemy abundance was higher in margins with many flowers than in margins with some or no flower, but this pattern did not extend into the adjacent fields (Fig. 2.2a). This effect was mostly caused by the response of the spiders. The highest-ranking model explaining spider abundance included distance to field margins, flower cover, fertilizer and insecticide application and interactions between distance and insecticide and distance and flower cover. However, this model performed only marginally better than the more parsimonious second-highest ranking model without the interaction between distance and insecticide (Δ AICc = 0.95, Table 2.1b and S2.1). Fig. 2.2b therefore illustrates the relationships based on this more conservative parsimonious model and shows spider abundance being higher in margins with many flowers than in margins with some or no flowers. This pattern extended 5 m into the field as well, but is no longer apparent at 10 and 20 m from the field edge. Spider abundance was furthermore higher in unfertilized and unsprayed fields (Fig. 2.3a, b). Carabid beetle abundance was best explained by the effects of distance, fertilizer, flower richness and distance × flower richness (Table 2.1c and S2.1). Six other high-ranking models performed almost equally well but were less parsimonious than the highest-ranking model (Table 2.1c), Consistent factors in all models were positive effects of distance, negative effects of fertilize, and a positive relationship with one of the flower variables. Fig. 2.2c illustrates the interacting relationship between flower richness and distance based on the highest-ranking model, with fields with flower-rich field margins having more carabids at the field edge but less in the crop field itself. The best model explaining staphylinid beetle abundance only included fertilizer which significantly promote its abundance (Table 2.1d and S2.1, Fig. 2.3d), however, this positive effects of fertilizer on staphylinid beetle was in contrast to that on spiders and carabid beetles.

Aphids

A total of 725 aphids were observed on wheat tillers, all during the heading (386) or flowering stage

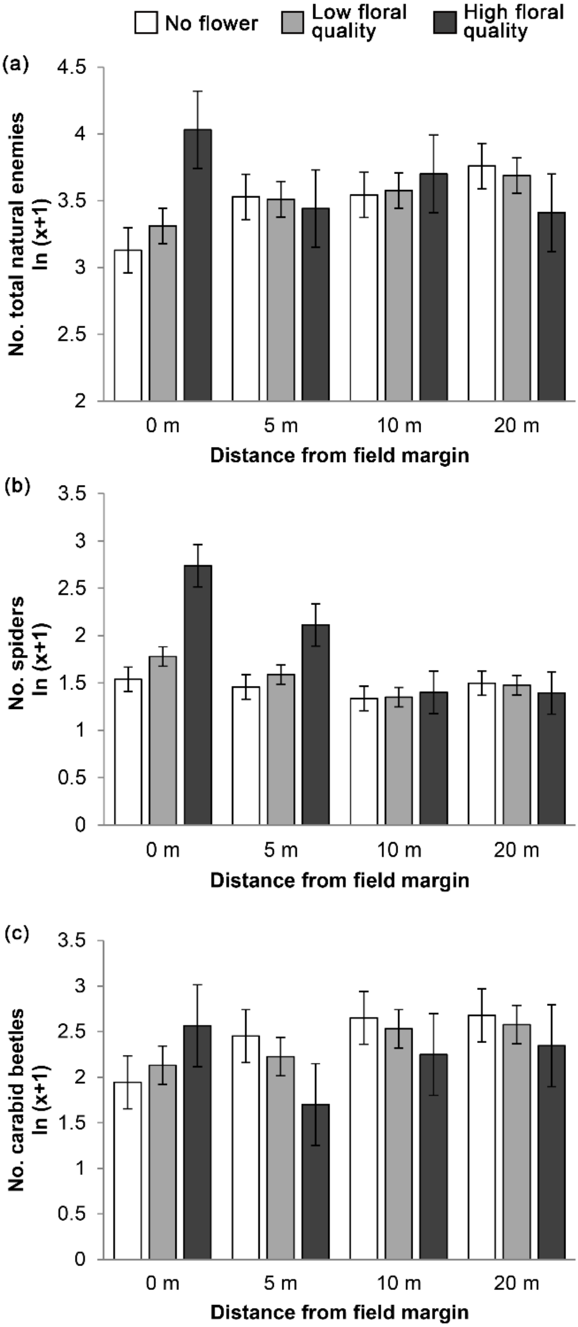

Fig. 2.2. Effects of floral quality and distance to field margins on mean abundance of (a) total natural enemies, (b) spiders and (c) carabid beetles in fields adjacent to margins with no flower (white, 10th quantile), low floral quality (light grey, 50th quantile) and high floral quality (dark grey, 90th quantile). For total natural enemies (a) and spiders (b), floral quality was defined as flower cover and for carabid beetles (c), floral quality was defined as flower species richness. Model-estimated means are shown, with error bars indicating SE.

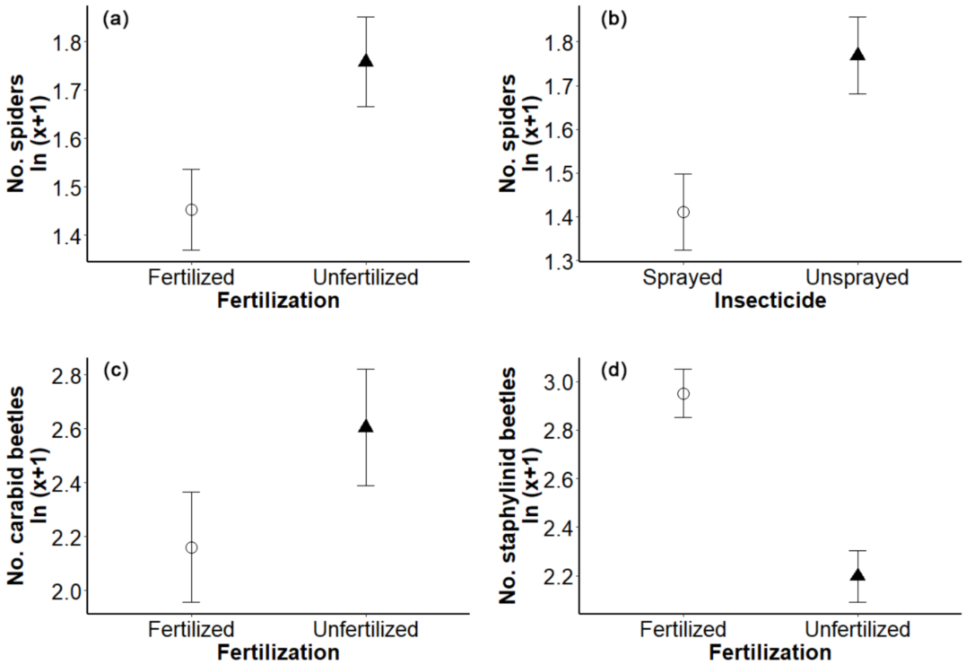

Fig. 2.3. Effects of on-field management on mean abundance of (a, b) spiders, (c) carabid beetles and (d) staphylinid beetles. Open circles represent intensive on-field management (fertilized or insecticide sprayed), filled triangles represent extensive on-field management (unfertilized or insecticide unsprayed). Model-estimated means are shown, with error bars indicating SE.

(339) of the wheat. The best model explaining the abundance of aphids only included insecticide which significantly reduced aphid numbers (Table 2.1e and S2.1, Fig. S2.2). The second-best model, whose Δ AICc was only 0.08, included a negative relationship of overall aphid numbers with flower cover, suggesting a potential contribution of wildflower strips to aphid control (Table 2.1e). However, this second-best model was far more complex than the insecticide-only model.

Wheat yield

Wheat yield was best explained by a model including fertilizer, distance, flower richness and the interaction between the last two factors (Table 2.1f and S2.1). Fertilizer application had the expected positive effect with a 48% yield reduction in unfertilized plots (Fig. 2.4a), Next to margins without flowers, wheat yield was 15% and 16% lower at 5 m than at 10 and 20 m from the margin respectively while next to flower-poor field margins, wheat yield was 10% lower at 5 m than at 10 and 20 m from the margin (Fig. 2.4b). In contrast, next to flower-rich margins wheat yield at 5 m was slightly higher

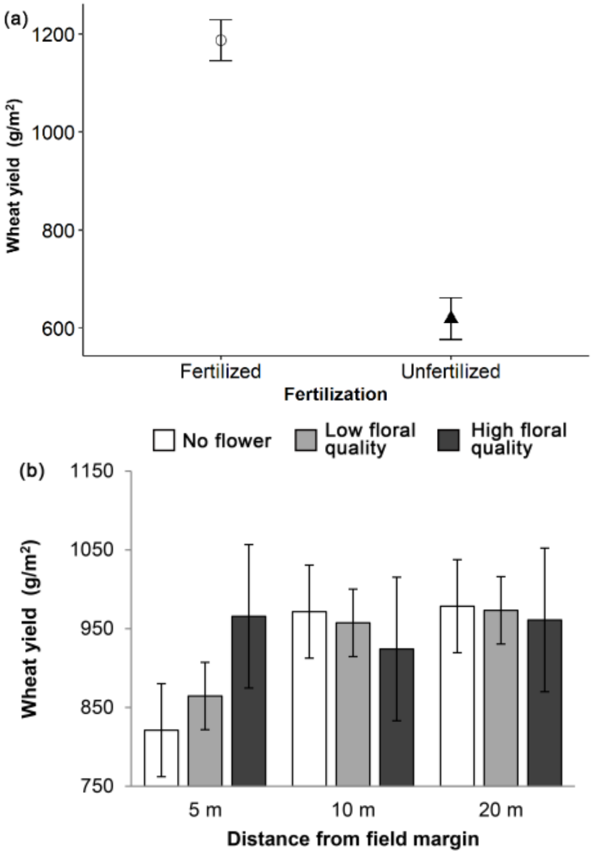

Fig. 2.4. (a) Effects of fertilization on mean wheat yield. Open circle represents fertilized fields and filled triangle represents unfertilized fields. (b) Effects of floral quality and distance to field margins on mean wheat yield in fields adjacent to margins with no flower (white, 10th quantile), low floral quality (light grey, 50th quantile) and high floral quality (dark grey, 90th quantile). Floral quality was defined as flower species richness. Model-estimated means are shown, with error bars indicating SE.

than yield at both 10 and 20 m from the margin. As a result, wheat yield at 5 m from flower-rich field margins was 15% and 10% higher than yields at 5 m from margins with no or some flowers respectively. These differences were no longer apparent at 10 and 20 m from the margins (Fig. 2.4b).

Discussion

The major result of our study is that it is not the establishment of wildflower strips that drives effects on ground-dwelling natural enemies and wheat yield, but it is the actual cover and diversity of wildflowers in field margins that determines effect size. These flowers can be introduced by establishment of wildflower strips but can also occur naturally in pre-existing field boundaries as well. Furthermore, we did not find any interactions between the effects of floral characteristics of field margins and those of on-field management on natural enemies, aphids and wheat yields indicating that in our study effects of wildflower strips were not masked by fertilizer or insecticide applications but were mainly additive.

The fact that presence of wildflower strips did not feature in any of the sets of candidate models was probably caused by the large variation in floral quality of the studied wildflower strips. Although on average flower cover and diversity were significantly higher in wildflower strips than in control field boundaries, there was considerable overlap, with the most flower-rich control boundary scoring better than three wildflower strips. Our results highlight that sowing wildflowers on farmland does not automatically result in high flower cover and diversity. The examined wildflower strips were supposed to be cut twice per year and cuttings had to be removed, such management is generally considered to promote wildflower cover (Piqueray et al., 2019). However, the high nutrient availability in the clayey arable soil could have made it difficult for wildflower species of non-local provenance to compete with the naturally occurring perennial grass species (Schmidt et al., 2019). Currently, schemes subsidizing farmers to establish biodiversity enhancing semi-natural landscape elements rarely include criteria regarding the quality that should be aimed for or management practices that should be implemented to provide successful outcomes (Cole et al., 2020). The results of our study suggest that including such criteria could not only increase biodiversity outcomes but also the delivery of ecosystem services regulating agricultural production.

Spiders and carabid beetles were positively related to cover and diversity of wildflowers respectively, this is unexpected since neither species group feeds on pollen or nectar. In a recent meta-analysis on the effects of wildflower strips, Albrecht et al. (2020) did not find a relationship between wildflower diversity and pest control services while the expected relationship between flower diversity and pollination services was indeed found. Natural enemies benefit from undisturbed overwintering sites, especially when there are no crops on the fields. Perennial wildflower strips can function as such and are known to support, for example, higher densities of carabid beetles than regularly disturbed crop edges (Ganser et al., 2019). More importantly, vegetation dominated by flowering forbs generally has a more open and complex vertical vegetation structure (Schmidt-Entling & Döbeli, 2009). The openness of the vegetation may allow beetles to move more easily through the vegetation while the more complex vertical structure provides more niches for invertebrates and allows, for instance, coexistence of higher densities of web-building and ground-dwelling spiders (Schmidt-Entling & Döbeli, 2009). Spiders could furthermore benefit from an increase in prey resources such as flower visiting insects that are attracted by the high flower cover (Dukas & Morse, 2003; Heiling et al., 2003). In sum, the promotion of abundance of spiders and carabid beetles was probably not driven by the floral food resources but by the more complex structure that flowers in field margins provided.

Interestingly, we did not find much support for interactions between the effects of floral resources in field margins and the effects of on-field management for any of the response variables suggesting that the two management strategies operated independently in our study. Staphylinid beetles were not affected by wildflower strips but their abundance in the field was positively affected by fertilizer application supporting earlier observations of Gagic et al. (2017). Abundance of spiders and carabid beetles was negatively related to fertilizer application and abundance of spiders was negatively related to insecticide applications. In the crop, the three groups of natural enemies thus all responded differently to wildflowers and on-field management. This may explain why recent meta-analyses find contrasting relationships between cover of semi-natural habitat and natural enemies in crops (Karp et al., 2018). Different species groups respond differently not only to the resources in semi-natural habitat, they also demonstrate different, sometimes opposite responses to on-field management. In this study carabid beetles were negatively affected by fertilizer application while staphylinid beetles were positively affected, effectively neutralizing any overall response by total natural enemies. In the crop, activity density of spiders declined but that of carabid beetles increased with increasing distance from the margin (Fig. 2b, c). As a result, activity density of the pooled number of natural enemies in the crop showed very little difference between treatments but increased from margin to field center at low flower cover while it declined at high flower cover (Fig. 2.2a). Pitfall traps measuring activity density are known to be more effective in open habitats where ground-active species can move more rapidly (Phillips & Cobb, 2005). The numbers of observed specimens in the field margin with dense vegetation are therefore probably an underestimation of their relative abundance of the three species groups at this location.

Any observed positive effects of flowers in the margins on invertebrates in the crop were restricted to a narrow 5-10-meter-wide zone along the field margin. This was also the zone where positive effects of wildflowers on crop yield were detected (Fig. 2.4b) which is in line with recent findings of Albrecht et al. (2020) that delivery of pest control services generally does not extend very far into the field. The best model explaining crop yield was very similar to the best model explaining total natural enemy abundance. The only differences were the obvious positive effects of fertilizer application on crop yield, and flower richness rather than flower cover being related to crop yield (Table 2.1). As flower cover and flower species richness were moderately correlated, this may suggest a relationship between natural enemy abundance and crop yield. The reason why we did not find any effects of insecticide on wheat yield may result from the fact that the insecticide treatment was applied regardless of the actual pest pressure in the plots. We did not test for direct relationships between natural enemies and yield because natural enemies generally concentrate on locations with the highest densities of pests (Ramsden et al.,

2015) which may lead to spurious correlations. The best model explaining aphid abundance did not include any wildflower variable and only insecticide application featured consistently in the candidate set of best models with aphid abundance being about 1.5 times higher in unsprayed fields than sprayed ones (Fig. S2.2). Insecticide spraying also negatively affected the abundance of spiders (Fig. 2.4b), one of the three most dominant natural enemy groups in this system. This confirms that insecticide application simultaneously reduces pests and some natural enemies (Bommarco et al., 2011; Regan et al., 2017) which may result in net effects on wheat yield that are not always positive. It is noteworthy that, compared to the field center, we did not observe higher yields in crop edges next to flower rich vegetation. The crops showed a typical reduction in yield towards the edge of the field when a margin contained no or few flowers. This yield depression was absent next to flower rich-field margins (Fig. 2.4b). A possible explanation could be that margins without any flowering forbs are a source of more pests than natural enemies while the reverse is true for flower-rich margins. Furthermore, pest species and groups of natural enemies that were not included in this study such as cereal leaf beetles and lacewings may also have affected the yield patterns observed in our study (Tschumi et al., 2015). Our results indeed suggest that the observed relationship between crop yield and field margin wildflowers originated from the impact of a wider set of natural enemies on a wider set of pest species than we sampled (Wäckers & van Rijn, 2012; Hatt et al., 2017).

Conclusion

Previous studies examining the effectiveness of wildflower strips in enhancing pest control services have focused on evaluating the effects of presence of wildflower strips and often excluded strips from analyses when mixtures failed to establish or wildflowers were overgrown by spontaneous weedy vegetation (e.g., Tschumi et al., 2015; Tschumi et al., 2016b). While such an approach gives valuable information on the potential of this management practice and provides a proof-of-concept, it fails to include variables that influence effectiveness under real-world conditions and does not consider the way in which they are typically being established and managed by farmers (Kleijn et al., 2006). The wildflower strips examined in this study were part of a government funded agri-environment scheme and were established and managed following the guidelines of that scheme. The fact that many of these strips comprised few wildflowers, sometimes even less than the pre-existing field boundary, is therefore a meaningful and important result. It suggests that more attention should be given to environmental factors impacting the quality of wildflower strips, which management practices can be used to enhance floral resources and how this can be incorporated into agri-environmental scheme design and prescriptions (Cole et al., 2020). A better understanding of how to enhance the desirable species, and to suppress the unwanted species in wildflower strips may furthermore reduce the reluctance of farmers to implement this measure (Kleijn et al., 2019) and possibly increase its uptake in agricultural landscapes. It furthermore suggests that management increasing flower cover and diversity in pre-existing field boundaries may be just as effective for ecosystem service delivery as establishing new wild flower strips. Since there are little or no opportunity costs associated with biodiversity enhancing management of the herbaceous vegetation in the linear landscape elements and such elements make up the green infrastructure in agricultural landscapes, this may be a much more cost-effective approach to improve ecosystem services regulating agricultural production than taking productive land out of production to sow wildflowers.

Acknowledgements

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Supplementary materials

Table S2.1. Significance test for the most parsimonious models explaining abundance of different groups of natural enemies and aphids, and wheat yield. Dx, distance from field margins (5 m, 10 m and 20m); F, fertilizer application (yes/no); I, insecticide application (yes/no); FC, flower cover; FR, flower species richness. (Asterisks indicate significance at *P < 0.05; **P < 0.01; ***P < 0.001).

Explanatory variables	Estimate	Standard error	d.f.	t value	Pr(>|t|)	
Total Natural enemies						
(Intercept)	3.378	0.125	27.57	27.079	<0.001	***
FC	0.645	0.255	26.08	2.535	0.018	*
D_{5}	0.112	0.098	174.00	1.138	0.257	
D_{10}	0.190	0.098	174.00	1.930	0.055	
D_{20}	0.255	0.098	174.00	2.593	0.010	*
FC×D_{5}	-0.702	0.197	174.00	-3.565	<0.001	***
FC×D_{10}	-0.536	0.197	174.00	-2.723	0.007	**
FC×D_{20}	-0.916	0.197	174.00	-4.648	<0.001	***
Spiders						
(Intercept)	1.890	0.095	59.36	19.900	<0.001	***
F	-0.311	0.106	45.18	-2.936	0.005	**
I	-0.358	0.104	40.57	-3.442	0.001	**
FC	0.853	0.191	54.96	4.465	<0.001	***
D_{5}	-0.239	0.114	174.00	-2.092	0.038	*
D_{10}	-0.531	0.114	174.00	-4.653	<0.001	***
D_{20}	-0.419	0.114	174.00	-3.669	<0.001	***
FC×D_{5}	-0.386	0.229	174.00	-1.687	0.093	
FC×D_{10}	-0.805	0.229	174.00	-3.518	<0.001	***
FC×D_{20}	-0.925	0.229	174.00	-4.04	<0.001	***
Carabid beetles						
(Intercept)	2.152	0.197	23.12	10.885	<0.001	***
F	-0.444	0.165	44.17	-2.695	0.010	**
FR	0.442	0.402	22.30	1.099	0.284	
D_{5}	0.048	0.134	174.00	0.357	0.721	
D_{10}	0.365	0.134	174.00	2.720	0.007	**
D_{20}	0.414	0.134	174.00	3.093	0.002	**
FR×D_{5}	-0.980	0.269	174.00	-3.645	<0.001	***
FR×D_{10}	-0.732	0.269	174.00	-2.720	0.007	**
FR×D_{20}	-0.681	0.269	174.00	-2.531	0.012	*
Staphylinid beetles						
(Intercept)	2.613	0.082	16.62	31.164	<0.001	***
F	0.750	0.103	229.03	7.274	<0.001	***
Aphids						
(Intercept)	1.253	0.148	16.53	8.445	<0.001	***
I	-0.472	0.112	42.58	-4.192	<0.001	***
Yield						
(Intercept)	869.41	39.95	19.95	21.761	<0.001	***
F	597.87	23.61	43.34	24.054	<0.001	***
D_{10}	86.25	21.82	116.00	3.952	<0.001	***
D_{20}	103.18	21.82	116.00	4.728	<0.001	***
FR	103.38	81.63	19.54	1.266	0.220	
FR×D_{10}	-137.23	43.77	116.00	-3.135	0.002	**
FR×D_{20}	-115.80	43.77	116.00	-2.645	0.009	**

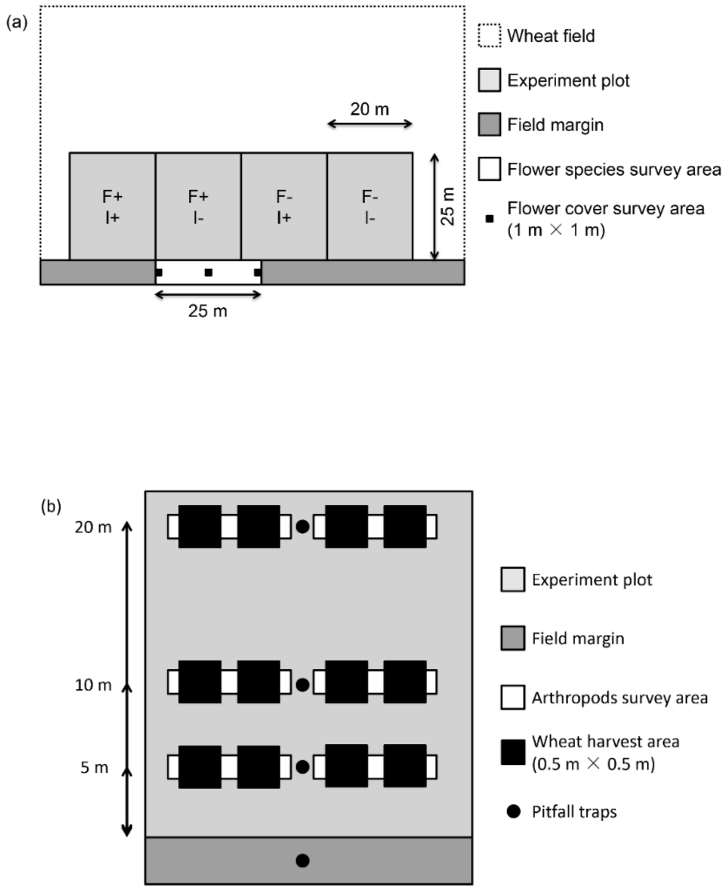

Fig. S2.1. (a) Set-up of experimental plots per field site and close-up of locations of survey transects. (b) Subplots for wheat harvesting for per experimental plot.

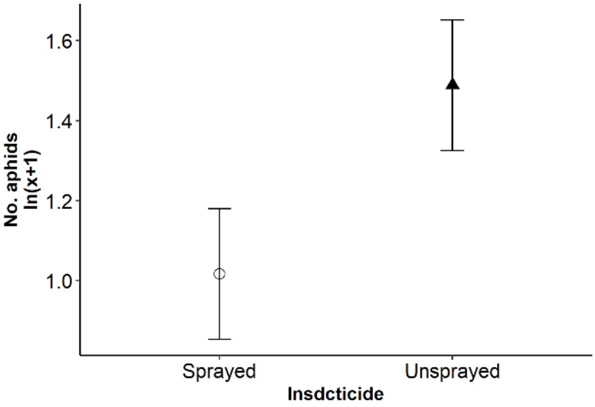

Fig. S2.2. Effects of on-field management on mean abundance of aphids. Open circle represents insecticide sprayed fields and filled triangle represents insecticide unsprayed fields. Model-estimated means are shown, with error bars indicating SE.

Chapter 3

Inconsistent responses of carabid beetles and spiders to land-use intensity and landscape complexity in north-western Europe

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Abstract

Reconciling biodiversity conservation with agricultural production requires a better understanding of how key ecosystem service providing species respond to agricultural intensification. Carabid beetles and spiders represent two widespread guilds providing biocontrol services. Here we surveyed carabid beetles and spiders in 66 winter wheat fields in four northwestern European countries and analyzed how the activity density and diversity of carabid beetles and spiders were related to crop yield (proxy for land-use intensity), percentage cropland (proxy for landscape complexity) and soil organic carbon content, and whether these patterns differed between dominant and non-dominant species. Less than 17% of carabid or spider species were classified as dominant, which accounted for more than 90% of individuals respectively. We found that carabids and spiders were generally related to different aspects of agricultural intensification. Carabid species richness was positively related with crop yield and evenness was negatively related to crop cover. The activity density of non-dominant carabids was positively related with soil organic carbon content. Meanwhile, spider species richness and non-dominant spider species richness and activity density were all negatively related to percentage cropland. Our results show that practices targeted to enhance one functionally important guild may not promote another key guild, which helps explain why conservation measures to enhance natural enemies generally do not ultimately enhance pest regulation. Dominant and non-dominant species of both guilds showed mostly similar responses suggesting that management practices to enhance service provisioning by a certain guild can also enhance the overall diversity of that particular guild.

Key words

dominant species; ecological intensification; evenness; natural enemies; pest control service; soil organic carbon

Introduction

In Europe, farming and biodiversity conservation have always been tightly interlinked (Batáry et al., 2015). Over the course of thousands of years of traditional extensive farming practices, many species have adapted to human disturbance and have even come to depend on agricultural habitats (Sutcliffe et al., 2015). However, the intensification of agriculture with high inputs of anthropogenic chemicals and homogenization of agricultural landscapes has negatively impacted farmland biodiversity and currently threatens many species (Goulson et al., 2015; Gámez-Virués et al., 2015; Emmerson et al., 2016; Dainese et al. 2019). Recent attempts to make modern farming more sustainable, such as ecological intensification (Bommarco et al., 2013), rely on promoting the ecosystem services provided by communities of species that occur naturally on farmland. More diverse communities of service-providing organisms often provide higher levels of services as different species occupy different niches and complement each other (Letourneau et al., 2009; Ollerton, 2017; Dainese et al., 2019; Snyder, 2019). Furthermore, higher evenness of functional groups can also promote service provisioning because more even communities occupy each niche more completely (Crowder et al., 2010; Aldebron et al., 2020; Yuan et al., 2019, but see Dainese et al., 2019). Maintaining high biodiversity levels on farms could thus serve both biodiversity conservation and ecosystem service provisioning, thereby potentially making agricultural production more sustainable (Tscharntke et al., 2012).

However, Kleijn et al. (2011) argued that the species providing most of the services to farming are different species than the species that are threatened in their existence. Different management practices are therefore required when aiming at enhancing ecosystem service provisioning or conserving rare species. For example, crop pollination is mainly provided by a relatively small set of dominant bee species, while the contribution of threatened bee species is negligible (Kleijn et al., 2015; Winfree et al., 2015). These dominant crop pollinators are generally robust to land-use change, being able to persist even in intensively managed agricultural landscapes, and can relatively easily be promoted by generic, local-scale conservation measures (Kleijn et al., 2015). In contrast, non-dominant or rare bee species are often more susceptible to agricultural intensification and loss of semi-natural habitats (Fijen et al., 2019; Harrison et al., 2019), and the conservation of these species typically requires more targeted conservation measures and landscape-scale approaches (Pywell et al., 2012; Senapathi et al., 2015).

While in recent years our understanding of how dominant and non-dominant crop pollinating species respond to environmental change has greatly advanced, we know much less about this for natural enemies that provide pest control services, another key ecosystem service to crops (Bianchi et al., 2006; Losey & Vaughan, 2006). As far as we know, very limited studies have examined whether dominant and non-dominant natural enemies respond differently to environmental drivers. To date, most studies have focused on responses in richness and abundance of the entire species pool with only a small proportion of studies distinguishing between rare and common species or generalist and specialist species (Desender & Bosmans, 1998; Niemelä, 2001; Desender et al., 2010).

Predatory natural enemies generally come from a wider range of different arthropod orders and families (e.g. beetles, wasps, lacewings, hoverflies and spiders) and have more variation in life history traits than pollinators. This can partly explain the lack of a general framework for landscape and local scale drivers of natural enemy diversity or abundance (Karp et al., 2018; Martin et al., 2019; Mei et al., 2021). For example, while many natural enemies are positively related to landscape-scale cover of semi-natural habitat (Chaplin-Kramer et al., 2011), some species groups (e.g., coccinellid beetles and spiders) have been shown to be positively related to cover of cropland (Rand & Tscharntke, 2007). Even species within the same taxon but with different ecological traits can display different response patterns. For instance, Duan et al. (2019) found that ground-hunting spiders and predatory carabids were more sensitive to the decline of the area of suitable habitats than aerial dispersing spiders and small-sized omnivorous carabids. Furthermore, species groups could be differently affected by local land-use intensity as well, as illustrated by spiders and carabid beetles responding negatively to fertilizer application but staphylinid beetles responding positively (Gagic et al., 2017; Mei et al., 2021). Within species groups, local land-use intensity could also alter species evenness, as for example shown by Li et al. (2018) who found that higher total nitrogen input decreased the species richness of spiders while total abundance was unaffected, resulting in spider assemblages being more dominated by a small subset of species.

Effects of local land-use intensity and landscape composition can furthermore be moderated by local soil characteristics. Soils with high organic matter content can provide alternative food resources when prey levels in the crop are low, thereby supporting more stable populations of natural enemies (Birkhofer et al., 2008; Aguilera et al., 2021). High soil organic matter also helps to shape complex soil structure (Bulluck et al., 2002), which potentially provides more spatial niches for natural enemies. By providing these additional resources, fields with high soil organic matter content can therefore mitigate the negative effects of on-field management and landscape simplification on natural enemies (Riggi & Bommarco, 2019; Redlich et al., 2021). However, to date little is known about how landscape complexity, land-use intensity and soil organic matter jointly shape natural enemy communities on agricultural fields, and whether responses differ for dominant and non-dominant species, hindering the design of more targeted conservation strategies.

Here we used data on natural enemy communities in 66 paired winter wheat fields in four northwestern European countries (Germany, the Netherlands, Sweden and United Kingdom) to investigate the response of natural enemy communities to landscape complexity, local land-use intensity and soil organic matter content, and specifically examined whether and how responses differ between dominant and non-dominant species. We focused on carabid beetles and spiders as they represent the two groups of natural enemies in arable fields in northwestern European and widely used as bioindicators (Lang et al., 1999; Borchard et al., 2014). We used pitfall traps to collect carabids and spiders in field pairs that covered a gradient in land-use intensity and landscape complexity, with fields within pairs having contrasting soil organic carbon content. We asked 1) how activity density, species richness and evenness of total carabid beetles and spiders are related to local land-use intensity and landscape complexity; 2) whether these relationships are affected by different soil organic carbon content, and 3) whether the response patterns differ between dominant and non-dominant species.

Methods

Experimental design

In 2014, we selected eight pairs of winter wheat fields in the Netherlands, Sweden and United Kingdom and nine pairs in Germany, resulting in 33 pairs in total. The sites were a subset of the data used by Gagic et al. (2017) for which we were able to obtain species level data of carabid beetles and spiders. All of the fields were conventionally managed. The paired fields were selected to have contrasting levels of soil organic carbon, resulting from differences in management history such as use of organic or mineral fertilizers as well as different crop rotation or tillage practices, the fields within a pair were selected to have similar landscape complexity and soil condition (e.g., pH and soil texture) as far as possible. Except in the Netherlands, field sites were closer to their paired field than to fields in other pairs (Table S3.1). Due to high soil variability in the Netherlands, to ensure pairs had matching soil type and local landscape context, it was not always possible to pair fields geographically, thus all fields were located in a single study region. We took soil samples to validate that soil organic carbon (SOC) content levels differed within field pairs. In each field, we randomly collected five soil samples at a distance of 5-8 m from the crop edge before the first fertilizer application by farmers which were then pooled and mixed. Mean SOC content in Germany was 1.63% (SD ± 1.03) for high sites and 1.20% (SD ± 0.49) for low sites; the Netherlands, averaged 2.00% (SD ± 0.23) in high sites and 1.39% (SD ± 0.30) in low sites; in Sweden, high sites had 4.44% (SD ± 1.11) SOC and low sites 2.90% (SD ± 0.42); in the United Kingdom, high sites had 1.48% (SD ± 0.57) and low sites 1.05% (SD ± 0.30). Because the differences between paired high and low SOC content sites turned out to be relatively small, for this study we decided to include SOC content as a continuous variable rather than a factorial one.

The field pairs were selected across a gradient in landscape complexity, estimated as the percentage of cropland within a 1-km radius around each study field. The percentage of cropland is often used to quantify landscape complexity and is generally negatively correlated with it (Rusch et al., 2016; Martin et al., 2019).

In each field, we selected a study plot that was at least 12 × 14 m in size, with the longer side bordering a field boundary, and at least 10 m away from the nearest field corner. Within each pair, the field boundary characteristics were selected to be similar (e.g., to avoid that one field had a field boundary with a high plant richness while the other field had a field boundary with low plant richness). One of the objectives of the original study was to experimentally examine the impacts of fertilizer and pesticide applications (Gagic et al., 2017). For this purpose, each plot was subdivided into four subplots to which four treatments were randomly assigned: all combinations of presence or absence of the experimental application of insecticides and fertilizers. Insecticides were pyrethroid (broad spectrum) and applied once by using backpack sprayers in May in Germany, the Netherlands and Sweden and in June in the United Kingdom. Fertilizers were ammonium nitrate based and were applied three times in Germany and the UK, twice in Sweden and once in the Netherlands. Insecticides and fertilizers were applied by project members and were consistent with the typical type, amount and frequency within each country and in accordance with local recommended rates (Table S3.1). Farmers were allowed to use herbicides and fungicides in the treatment plots.

We used wheat yield as an indicator of local land-use intensity as this represents the end result of all short- and long-term management practices (Dietrich et al., 2012; Gabriel et al., 2013; Winqvist et al., 2014). Wheat was manually harvested in four randomly located subplots of 0.25 m^2 each. The harvested grains were air dried to approximately 14% moisture content and then weighted, expressed as grain dry weight per hectare (t/ha).

Surveying ground-dwelling arthropods

Pitfall traps (polypropylene beakers 155 mm high and 95 mm across) were used to survey ground-dwelling arthropods during the wheat flowering season (late May to early June). We placed one pitfall trap in the center of each treatment subplot at least 10 m from the field edge and filled it with 200 mL of a mixed solution of 2/3 water and 1/3 glycol and a drop of detergent to lower surface tension. A square aluminum plate was placed approximately 10 cm above each pitfall trap to prevent flooding by rain. Pitfall traps were opened for 10 days. All of the collected arthropods were stored in 70% ethanol solution for later identification. For the purpose of our study, the two most abundant species groups, carabid beetles (Carabidae) and adult spiders (Araneae), were selected as our bioindicators and they were counted and identified to species level using standard keys (Hackston, 2020; Nentwig et al., 2021). We determined the diet preference of each carabid beetle species based on Larochelle (1990) and the hunting strategy of all observed spider species based on Cardoso et al. (2011) following Gallé et al. (2019). Furthermore, because the arthropod communities will inevitably differ in composition between countries, we classified the carabids or spiders as nationally dominant and non-dominant species based on whether species made up respectively more or less than 5% of the total number of individuals caught of each species group in a country following Kleijn et al. (2015).

Statistical analysis

All analyses were performed using R version 4.2.0 (R Core Team, 2022a). Since the focus of our study was on across-field effects of land-use intensity, not on the subplot-scale effects of the different experimental management treatments (which had already been examined by Gagic et al., 2017), we pooled the collected carabid beetles and spiders over the different treatments and we averaged the wheat yield across all four treatments per field to use it as indicator of local land-use intensity. Because each field had been subjected to the same combination of treatments and earlier analyses showed that the effects of these treatments on carabid beetle and spider activity density were generally not influenced by the environmental variables (Appendix 3 of Gagic et al., 2017), we are confident that pooling the samples didn’t affect the relationships of the environmental variables across fields.

Our response variables included activity density, species richness and evenness of all carabid beetles and spiders, and activity density and species richness of dominant and non-dominant carabids and spiders respectively. We calculated Evar index based on the observed number of individuals to describe the community evenness, this index is independent from species richness thus measured the true evenness of each site and suitable for meta-analysis (Smith & Wilson, 1996). E_{var} ranges from 0 (maximally uneven) to 1 (perfectly even). Evenness was only calculated for sites with more than 5 individuals, as evenness values for sites with fewer individuals are not very reliable and have strong influence on response patterns. Our explanatory variables included wheat yield as an indicator of land-use intensity, percentage cropland as an indicator of landscape complexity and SOC content. We used an information theoretic approach, with which we can assess the relative importance of explanatory variables based on a candidate set of best models. For landscape-scale studies that examine multiple hypotheses simultaneously, this is generally preferred over inferring significant relationships with explanatory variables from a single best model (Grueber et al., 2011) and the information theoretic approach is now becoming rapidly accepted as a more robust approach for many kinds of complex ecological studies (e.g., Knapp et al., 2022; Bishop et al., 2023). First, generalized linear mixed models (GLMM, package glmmTMB; Magnusson et al., 2021) with the appropriate error distribution and link function for each response variable were constructed (Table 3.1). To be able to generalize observed patterns within countries, we mean-centered SOC, wheat yield and proportion of cropland within each country (van de Pol & Wright, 2009). The within-country centered explanatory variables were subsequently scaled (centered data divided by two standard deviations) across the entire dataset as this would allow us to use the effect sizes of predictors to compare their relative importance (using R package ‘standardize’; Eager, 2021). For each response variable, we constructed a global model containing the three standardized explanatory variables and all their two-way interactions as fixed factors and field pair nested in country as random factors. To check for multicollinearity of explanatory variables, we calculated variance inflation factors (VIF; Draper & Smith, 1998) of all full models. The highest VIF was 1.05, which is well below the threshold of 3 (Zuur et al., 2007). Next, for each response variable we constructed an all-subsets model set consisting of all possible combinations of the fixed factors and their two-way interactions, using the function “dredge” from the R package MuMIn (Bartoń, 2020). We first ranked the models in the model set based on their Akaike Information Criterion values corrected for small sample size (AICc) and calculated full-model averaged parameter estimates and parameter weights (or variable importance; i.e., the probability that a given explanatory variable appears in the most appropriate model) based on all models with Δ AICc < 2 (Burnham et al., 2011). The best supported relationships (based on variable importance and the confidence interval of the effect size not overlapping zero) were visualized using R package “visreg” (Breheny & Burchett, 2020).

Results

Overall, we collected 3284 carabid beetles belonging to 63 species and 2730 adult spiders belonging to 71 species and 15 families. Carabid beetle activity density was highest in Sweden (2106 individuals belonging to 36 species), followed by Germany (485 individuals and 29 species), United Kingdom (456 and 20) and the Netherlands (237 and 18) (Table 3.2). Adult spider activity density was highest in Germany (1237 individuals and 50 species), followed by Sweden (1066 and 39), the Netherlands (288 and 14) and the United Kingdom (139 and 19) (Table 3.3).

Total carabid species richness in wheat fields was best explained by crop yield (variable importance $\omega = 1.00$), with species richness increasing with crop yield (model-averaged coefficient $\beta = 0.228$; Table 3.1; Fig. 3.1a). There was little support for relationships between total carabid beetle activity density and any of the explanatory variables (the candidate set of models that were within Δ AICc < 2 of the best models included the intercept-only model which indicates that none of the explanatory variables makes a meaningful contribution to explaining the response variable; Table S3.2), but total carabid beetle evenness was negatively related to the percentage cropland in a 1 km radius ($\beta = -0.097$; Fig. 3.1b). Additionally, carabid beetle evenness tended to increase with increasing SOC content ($\beta = 0.071$; $\omega = 1.00$), but the 95% confidence interval of the model averaged coefficient overlapped zero (Table

3.1). There was strong support for a positive relationship between SOC content and the activity density of non-dominant carabid species (β = 0.675; Fig. 3.1c).

Table 3.1. Results for generalized linear mixed models examining the effects of soil organic carbon content (SOC), proportion of cropland within 1-km radius (Lcrop), crop yield (Yield) and their interactions on diversity of carabids and spiders. Model averaged parameter estimates (β) and 95% confidence intervals (95% CI) are given for each explanatory variable included in the candidate set of best models (Δ AICc < 2, Table S3.2), predictors with confidence intervals not overlapping zero are indicated in bold. Relative importance (ω, sum of model weights including that predictor) of each predictor is given. Distribution and link function of GLMMs: G, Gaussian distribution with identity link function; P, Poisson distribution with log link function; NB, negative binomial distribution with log link function; zero-inflated, models with zero inflation.

Guild	Group	Diversity index	Distribution and link function	Predictor	β	95% CI	ω
Carabids	Total	Activity density	NB	(Intercept)	3.448	2.626 to 4.270	-
				SOC	0.203	-0.468 to 0.874	0.43
				Lcrop	0.193	-0.302 to 0.688	0.53
				Yield	0.016	-0.157 to 0.189	0.10
				SOC × Lcrop	-0.282	-1.508 to 0.944	0.21
		Species richness	P	(Intercept)	1.767	1.285 to 2.250	-
				SOC	0.125	-0.130 to 0.379	0.65
				Lcrop	-0.021	-0.143 to 0.101	0.21
				Yield	**0.228**	**0.030 to 0.426**	**1**
		Evenness	G	(Intercept)	0.527	0.471 to 0.584	-
				SOC	0.071	-0.060 to 0.202	1
				Lcrop	**-0.097**	**-0.175 to -0.018**	**1**
				SOC × Lcrop	0.129	-0.140 to 0.398	0.61
	Dominant	Activity density	NB	(Intercept)	3.145	2.278 to 4.011	-
				SOC	0.173	-0.487 to 0.834	0.29
				Lcrop	0.312	-0.327 to 0.951	0.66
				SOC × Lcrop	-0.456	-2.066 to 1.154	0.29
		Species richness	G	(Intercept)	3.080	1.919 to 4.241	-
				Yield	0.372	-0.368 to 1.112	0.63
	Non-dominant	Activity density	NB	(Intercept)	1.797	1.097 to 2.498	-
				SOC	**0.675**	**0.122 to 1.228**	**1**
				Lcrop	-0.020	-0.234 to 0.194	0.35
				SOC × Lcrop	-0.337	-1.407 to 0.733	0.35
		Species richness	P	(Intercept)	1.079	0.528 to 1.629	-
				SOC	0.261	-0.146 to 0.668	0.76
				Lcrop	-0.041	-0.251 to 0.168	0.25
				Yield	0.131	-0.196 to 0.459	0.53
Spiders	Total	Activity density	NB	(Intercept)	3.403	2.597 to 4.209	-
				Lcrop	-0.134	-0.488 to 0.220	0.52
				Yield	-0.117	-0.423 to 0.189	0.55
				Lcrop × Yield	-0.279	-1.105 to 0.547	0.36
		Species richness	G	(Intercept)	7.812	4.111 to 11.513	-
				Lcrop	**-2.638**	**-4.048 to -1.227**	**1**
				Yield	-0.236	-1.301 to 0.829	0.51
				Lcrop × Yield	-0.940	-4.110 to 2.231	0.32

Continued Table 3.1

Guild	Group	Diversity index	Distribution and link function	Predictor	β	95% CI	ω
Spiders	Total	Evenness	G	(Intercept)	0.578	0.470 to 0.686	-
				SOC	0.038	-0.065 to 0.141	0.51
				Yield	-0.0002	-0.033 to 0.032	0.18
				SOC × Yield	0.031	-0.113 to 0.175	0.18
	Dominant	Activity density	NB	(Intercept)	3.204	2.477 to 3.932	-
				Lcrop	-0.049	-0.299 to 0.200	0.27
				Yield	-0.134	-0.488 to 0.219	0.56
				Lcrop × Yield	-0.242	-1.101 to 0.616	0.27
		Species richness	G (zero-inflated)	(Intercept)	3.881	2.962 to 4.799	-
				Lcrop	-0.285	-0.900 to 0.331	0.61
				Yield	-0.284	-0.875 to 0.307	0.63
				Lcrop × Yield	-0.140	-0.903 to 0.623	0.17
	Non-dominant	Activity density	NB	(Intercept)	1.548	0.373 to 2.723	-
				SOC	-0.061	-0.366 to 0.244	0.22
				Lcrop	**-0.594**	**-0.982 to -0.206**	**1**
				Yield	-0.045	-0.296 to 0.206	0.58
				Lcrop × Yield	-0.531	-1.605 to 0.542	0.58
		Species richness	P	(Intercept)	1.041	0.140 to 1.942	-
				Lcrop	**-0.433**	**-0.676 to -0.190**	**1**

Species richness of all spiders and non-dominant spider species richness and activity density were all strongly negatively related to the proportion of cropland within a 1 km radius (Table 3.1; Fig. 3.1d, e, f). There was little support for any of the explanatory variables being related to the activity density of all spiders (the 95% confidence intervals of all model averaged coefficients overlapped zero and the candidate model set that were within Δ AICc < 2 of the best models included the intercept-only model; Table S3.2). This mainly reflected the lack of response of the activity density of dominant spiders, which made up majority of all collected spiders, to any of the explanatory variables. The non-dominant spider activity density was negatively related with the proportion of cropland (β = -0.594). Spider community evenness was not strongly related with any of the explanatory variables.

Discussion

Increasing land-use intensity and homogenization of agricultural landscapes have been found to be two important drivers of overall natural enemy loss (Hendrickx et al., 2007; Barnes et al., 2014; Dainese et al., 2019). However, our results indicate that the situation may be more complex. Across four European countries, we found partly contrasting relationships with our proxies for land-use intensity and landscape complexity for the two most abundantly occurring groups of natural enemies: carabid beetles and spiders. We found strong support for a positive relationship between carabid beetle species richness

Table 3.2. Species list of carabid beetles in Germany (GE), the Netherlands (NL), Sweden (SE) and the United Kingdom (UK). Diet preference of each species is presented. Species that were classified as dominant in at least one country (>5% of total abundance in each country) are shown in bold.

No.	Species	Diet preference	GE	NL	SE	UK	Sum
1	***Trechus secalis***	carnivore	0	0	**745**	1	746
2	***Pterostichus melanarius***	omnivore	**87**	**50**	**434**	**112**	683
3	***Anchomenus dorsalis***	carnivore	**147**	3	**203**	**136**	489
4	***Poecilus cupreus***	carnivore	**52**	**129**	**270**	1	452
5	***Bembidion lampros***	carnivore	11	10	**137**	18	176
6	***Trechus quadristriatus***	carnivore	**71**	0	45	**41**	157
7	***Nebria brevicollis***	omnivore	0	0	2	**94**	96
8	***Pseudophonus rufipes***	omnivore	**32**	0	42	19	93
9	***Agonum muelleri***	carnivore	0	**12**	30	0	42
10	*Clivina fossor*	omnivore	0	7	35	0	42
11	*Demetrias atricapillus*	omnivore	0	0	30	10	40
12	*Amara similata*	omnivore	1	0	25	0	26
13	*Calathus fuscipes*	carnivore	13	0	4	5	22
14	*Bembidion obtusum*	omnivore	4	1	16	0	21
15	*Loricera pilicornis*	carnivore	16	1	1	2	20
16	*Harpalus affinis*	herbivore	5	8	6	0	19
17	*Carabus granulatus*	carnivore	1	1	14	0	16
18	*Amara plebeja*	omnivore	0	0	14	0	14
19	*Zabrus tenebrioides*	carnivore	12	0	0	0	12
20	*Microlestes minutulus*	carnivore	8	0	0	0	8
21	*Stomis pumicatus*	omnivore	3	0	5	0	8
22	*Patrobus atrorufus*	herbivore	0	4	4	0	8
23	*Carabus nemoralis*	carnivore	0	0	8	0	8
24	*Pterostichus niger*	carnivore	0	0	8	0	8
25	*Brachinus crepitans*	omnivore	7	0	0	0	7
26	*Notiophilus aquaticus*	carnivore	0	0	6	0	6
27	*Pterostichus strenuus*	carnivore	0	0	5	0	5
28	*Amara ovata*	omnivore	1	1	0	2	4
29	*Nebria salina*	omnivore	0	0	0	4	4
30	*Badister bullatus*	carnivore	1	0	0	2	3
31	*Bembidion femoratum*	omnivore	0	3	0	0	3

Continued Table 3.2

No.	Species	Diet preference	GE	NL	SE	UK	Sum
32	*Pterostichus vernalis*	carnivore	0	3	0	0	3
33	*Amara lunicollis*	omnivore	0	0	3	0	3
34	*Amara aulica*	omnivore	2	0	0	0	2
35	*Calathus ambiguus*	carnivore	2	0	0	0	2
36	*Notiophilus biguttatus*	carnivore	1	0	0	1	2
37	*Poecilus versicolor*	carnivore	0	1	1	0	2
38	*Amara familiaris*	omnivore	0	0	2	0	2
39	*Bembidion aeneum*	omnivore	0	0	2	0	2
40	*Notiophilus aesthuans*	carnivore	0	0	2	0	2
41	*Calathus micropterus*	carnivore	0	0	0	2	2
42	*Laemostenus terricola*	omnivore	0	0	0	2	2
43	*Leistus fulvibarbis*	omnivore	0	0	0	2	2
44	*Asaphidion flavipes*	carnivore	1	0	0	0	1
45	*Brachinus explodens*	carnivore	1	0	0	0	1
46	*Diachromus germanus*	herbivore	1	0	0	0	1
47	*Harpalus rubripes*	herbivore	1	0	0	0	1
48	*Harpalus tardus*	omnivore	1	0	0	0	1
49	*Molops piceus*	carnivore	1	0	0	0	1
50	*Ophonus azureus*	carnivore	1	0	0	0	1
51	*Poecilus lepidus*	carnivore	1	0	0	0	1
52	*Bembidion monticola*	omnivore	0	1	0	0	1
53	*Bembidion quadrimaculatum*	carnivore	0	1	0	0	1
54	*Harpalus latus*	omnivore	0	1	0	0	1
55	*Amara communis*	omnivore	0	0	1	0	1
56	*Bembidion guttula*	herbivore	0	0	1	0	1
57	*Harpalus quadripunctatus*	herbivore	0	0	1	0	1
58	*Harpalus smaragdinus*	herbivore	0	0	1	0	1
59	*Ophonus rufibarbis*	herbivore	0	0	1	0	1
60	*Pterostichus oblongopunctatus*	omnivore	0	0	1	0	1
61	*Synuchus vivalis*	carnivore	0	0	1	0	1
62	*Amara equestris*	herbivore	0	0	0	1	1

Continued Table 3.2

No.	Species	Diet preference	GE	NL	SE	UK	Sum
63	*Pterostichus madidus*	carnivore	0	0	0	1	1
	Total		485	237	2106	456	3284

Table 3.3. Species list of spiders in Germany (GE), the Netherlands (NL), Sweden (SE) and the United Kingdom (UK). Family and hunting strategy of each species are presented. Species that were classified as dominant in at least one country (>5% of total abundance in each country) are shown in bold.

No.	Species	Family	Hunting strategy	GE	NL	SE	UK	Sum
1	***Oedothorax apicatus***	Linyphiidae	active hunter	**602**	2	**178**	5	787
2	***Pardosa prativaga***	Lycosidae	active hunter	12	**40**	**257**	4	313
3	***Pachygnatha degeeri***	Tetragnathidae	web builder	48	4	**185**	**31**	268
4	***Erigone atra***	Linyphiidae	active hunter	**70**	**19**	**94**	5	188
5	***Agyneta rurestris***	Linyphiidae	web builder	**146**	0	21	1	168
6	***Pardosa palustris***	Lycosidae	active hunter	17	**35**	**88**	**22**	162
7	***Trochosa ruricola***	Lycosidae	active hunter	53	**58**	23	**11**	145
8	***Pardosa agrestis***	Lycosidae	active hunter	44	**84**	5	6	139
9	***Bathyphantes gracilis***	Linyphiidae	web builder	14	0	**62**	**20**	96
10	***Erigone dentipalpis***	Linyphiidae	active hunter	**88**	0	6	0	94
11	***Pardosa amentata***	Lycosidae	active hunter	6	**38**	38	0	82
12	*Tenuiphantes tenuis*	Linyphiidae	web builder	32	0	14	2	48
13	***Pardosa pullata***	Lycosidae	active hunter	1	2	17	**22**	42
14	*Porrhomma microphthalmum*	Linyphiidae	web builder	7	0	17	0	24
15	*Drassyllus lutetianus*	Gnaphosidae	active hunter	10	0	7	1	18
16	*Diplostyla concolor*	Linyphiidae	web builder	11	0	3	0	14
17	*Pardosa lugubris*	Lycosidae	active hunter	12	0	0	0	12
18	*Mermessus trilobatus*	Linyphiidae	active hunter	10	0	0	2	12
19	*Robertus arundineti*	Theridiidae	web builder	0	0	10	0	10
20	*Micrargus subaequalis*	Linyphiidae	active hunter	4	0	4	0	8
21	*Porrhomma convexum*	Linyphiidae	web builder	0	0	7	0	7
22	*Micaria pulicaria*	Gnaphosidae	active hunter	2	0	2	2	6
23	*Xysticus ulmi*	Thomisidae	active hunter	0	1	3	1	5
24	*Argenna subnigra*	Dictynidae	active hunter	4	0	0	0	4

Continued Table 3.3

No.	Species	Family	Hunting strategy	GE	NL	SE	UK	Sum
25	*Drassyllus pusillus*	Gnaphosidae	active hunter	3	0	1	0	4
26	*Araeoncus humilis*	Linyphiidae	active hunter	2	0	2	0	4
27	*Pisaura mirabilis*	Pisauridae	web builder	1	2	1	0	4
28	*Clubiona reclusa*	Clubionidae	active hunter	0	0	4	0	4
29	*Xysticus kochi*	Thomisidae	active hunter	3	0	0	0	3
30	*Zodarion italicum*	Zodariidae	specialist	3	0	0	0	3
31	*Pachygnatha clercki*	Tetragnathidae	web builder	2	0	1	0	3
32	*Pardosa paludicola*	Lycosidae	active hunter	0	0	3	0	3
33	*Haplodrassus minor*	Gnaphosidae	active hunter	2	0	0	0	2
34	*Walckenaeria atrotibialis*	Linyphiidae	active hunter	2	0	0	0	2
35	*Aulonia albimana*	Lycosidae	active hunter	2	0	0	0	2
36	*Pardosa riparia*	Lycosidae	active hunter	2	0	0	0	2
37	*Xerolycosa miniata*	Lycosidae	active hunter	2	0	0	0	2
38	*Neottiura bimaculata*	Theridiidae	web builder	2	0	0	0	2
39	*Zodarion rubidum*	Zodariidae	specialist	2	0	0	0	2
40	*Phrurolithus festivus*	Phrurolithidae	active hunter	1	0	1	0	2
41	*Oedothorax fuscus*	Linyphiidae	active hunter	1	0	0	1	2
42	*Alopecosa accentuata*	Lycosidae	active hunter	1	0	0	1	2
43	*Oedothorax retusus*	Linyphiidae	Active hunter	0	0	2	0	2
44	*Histopona torpida*	Agelenidae	web builder	1	0	0	0	1
45	*Drassodes pubescens*	Gnaphosidae	active hunter	1	0	0	0	1
46	*Drassyllus praeficus*	Gnaphosidae	active hunter	1	0	0	0	1
47	*Haplodrassus signifer*	Gnaphosidae	active hunter	1	0	0	0	1
48	*Trachyzelotes pedestris*	Gnaphosidae	active hunter	1	0	0	0	1
49	*Hahnia nava*	Hahniidae	web builder	1	0	0	0	1
50	*Bathyphantes parvulus*	Linyphiidae	web builder	1	0	0	0	1
51	*Pocadicnemis juncea*	Linyphiidae	active hunter	1	0	0	0	1
52	*Porrhomma errans*	Linyphiidae	web builder	1	0	0	0	1
53	*Phrurolithus minimus*	Phrurolithidae	active hunter	1	0	0	0	1
54	*Sibianor tantulus*	Salticidae	active hunter	1	0	0	0	1
55	*Asagena phalerata*	Theridiidae	web builder	1	0	0	0	1
56	*Ozyptila claveata*	Thomisidae	active hunter	1	0	0	0	1

Continued Table 3.3

No.	Species	Family	Hunting strategy	GE	NL	SE	UK	Sum
57	*Eratigena picta*	Agelenidae	web builder	0	1	0	0	1
58	*zygiella x-notata*	Araneidae	web builder	0	1	0	0	1
59	*Prinerigone vagans*	Linyphiidae	active hunter	0	1	0	0	1
60	*Ceratinella scabrosa*	Linyphiidae	active hunter	0	0	1	0	1
61	*Diplocephalus latifrons*	Linyphiidae	active hunter	0	0	1	0	1
62	*Dismodicus bifrons*	Linyphiidae	active hunter	0	0	1	0	1
63	*Porrhomma pygmaeum*	Linyphiidae	web builder	0	0	1	0	1
64	*Satilatlas britteni*	Linyphiidae	web builder	0	0	1	0	1
65	*Savignia frontata*	Linyphiidae	active hunter	0	0	1	0	1
66	*Stemonyphantes lineatus*	Linyphiidae	web builder	0	0	1	0	1
67	*Walckenaeria nudipalpis*	Linyphiidae	active hunter	0	0	1	0	1
68	*Segestria senoculata*	Segestriidae	web builder	0	0	1	0	1
69	*Achaearanea riparia*	Theridiidae	web builder	0	0	1	0	1
70	*Porrhomma cambridgei*	Linyphiidae	web builder	0	0	0	1	1
71	*Piratula uliginosa*	Lycosidae	active hunter	0	0	0	1	1
	Total			1237	288	1066	139	2730

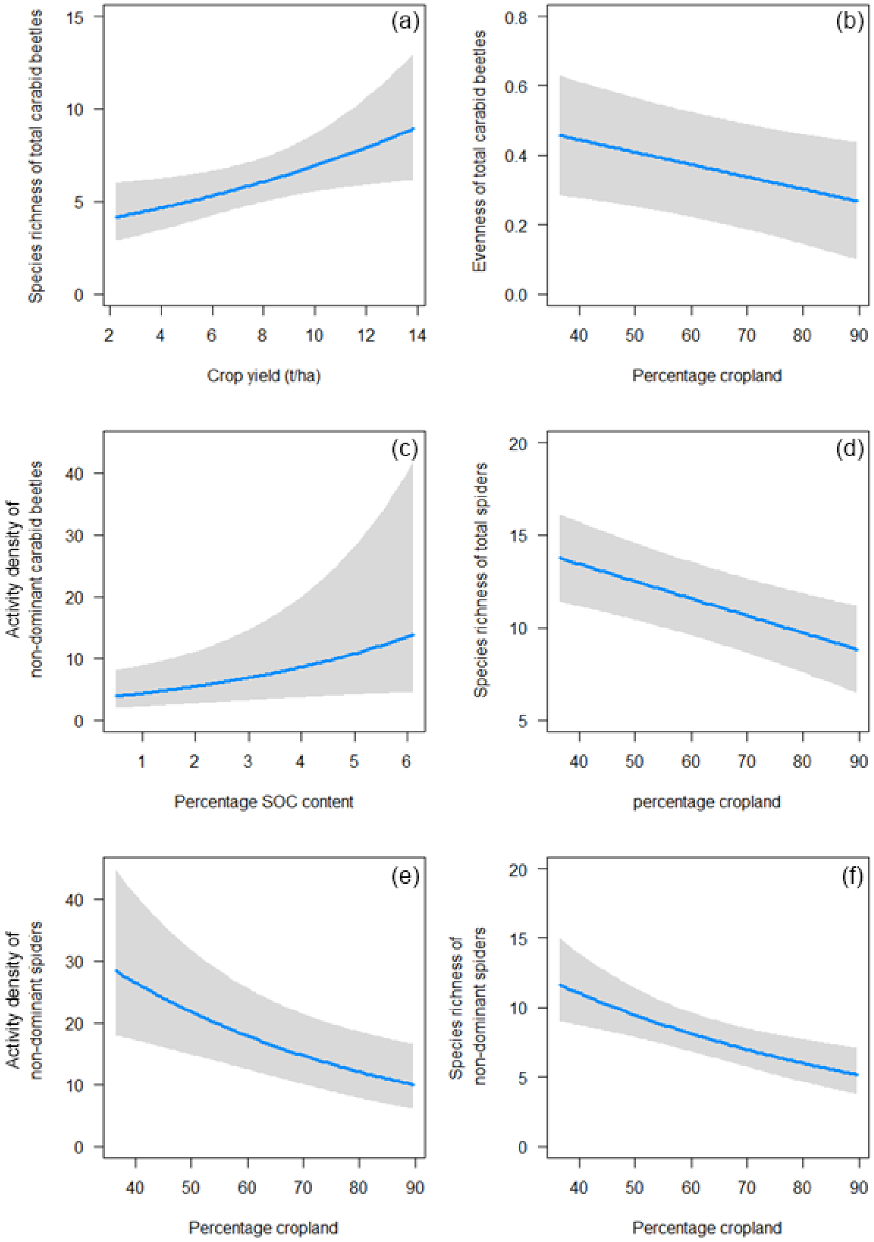

Fig. 3.1. A visualization of the relationships between different groups of carabid beetle and spider diversity and explanatory variables for which there was most support (high variable importance and confidence intervals of effect sizes not including zero). Panels show conditional partial regression plots of the relationships at the original scale of (a) species richness of carabid beetles and crop yield, (b) evenness of carabid beetles and percentage cropland in a 1 km radius, (c) activity density of non-dominant carabid beetles and SOC content and (d) spider diversity, (e) activity density of non-dominant spiders, (f) species richness of non-dominant spiders with percentage cropland in a 1 km radius. Fitted lines indicate the estimate effects and shaded areas indicate 95% confidence intervals.

and crop yield while carabid evenness was negatively related to percentage cropland in the landscape and tended to be positively related to soil organic carbon content. The activity density of non-dominant carabid beetles was furthermore positively related with soil organic carbon content. In contrast, spider species richness and non-dominant spider species richness and activity density were all negatively related to percentage cropland while there was no support for relationships with crop yield or soil organic carbon content. This indicates that measures that support spiders may not have the same effect on carabid beetles and vice versa. Our communities of carabid beetles and spiders were dominated by a few common species with less than 17% of the species accounting for more than 90% of the individuals.

In line with many previous studies, we found spiders were negatively related with landscape simplicity (Clough et al., 2005; Schmidt et al., 2005; Drapela et al., 2008; Batáry et al., 2012). Carabid beetles were not related with landscape simplicity. Winqvist et al. (2011) and Caballero-López et al. (2012) found carabid beetle activity density even to be positively related with landscape simplicity. This suggests that carabid beetles (especially dominant species) are less dependent on semi-natural habitats than spiders, although we found support for a negative relationship between landscape simplicity and carabid community evenness (Fig. 3.1b). A possible reason for the more consistent relationships with spiders than carabid beetles could be differences in diet preferences between the two guilds. Carabid beetle assemblages in cropland generally consist of carnivores, omnivores and herbivores while all spiders are strictly carnivorous (Duan et al., 2019; Gallé et al., 2019), this was also the case in our study (Table 3.2). This means that carabid beetles can utilize a wider range of food resources than spiders, making it easier for them to persist in cropland. Furthermore, many species of carabid beetles are known to lay eggs and spend their entire larval stages in arable soils (Lövei & Sunderland, 1996), suggesting they can complete their entire life cycle in cropland (Hanson et al., 2017; Boetzl et al., 2018). In contrast, the majority of spiders lay their eggs in sacs and hide the sacs in sheltered, undisturbed places or carry sacs with them while moving (Austin, 1985; Griswold, 1993). This makes arable fields relatively inhospitable places for spiders outside the crop growing season. At the start of each growing season, all spiders but not all carabid beetles therefore need to recolonize crop fields from the surrounding non-crop habitats (Öberg & Ekbom, 2006). Also, the multi-layered vegetation composed of trees, shrubs and grasses that can often be found in non-crop habitats provides a more complex vertical structure than crops, thus providing more spatial niches to simultaneously accommodate ground-dwelling and web-building spiders (Ditner et al., 2013; Garratt et al., 2017; Mestre et al., 2018). The negative relationships between proportion of cropland and evenness of total carabids, species richness and activity density of non-dominant spiders (but not for dominant spiders) seem to suggest that restoration of non-crop habitats in agricultural landscapes is especially beneficial for non-dominant species which generally include the species of conservation concern (Pywell et al., 2012).

The positive relationship between carabid beetle species richness and crop yield (Table 3.1, Fig. 3.1a), our proxy for land-use intensity, was somewhat unexpected as most previous studies have found negative relationships between land-use intensity indicators and activity density or species richness of carabids (Emmerson et al., 2016; Li et al., 2018; Wang et al., 2022). In another European cross-continental study Winqvist et al. (2014) found neutral to negative relationships between wheat yield and carabid beetle species richness and activity density. We cannot entirely rule out the possibility that the positive relationship between yield and carabid beetles in our study was driven by the carabids having a positive effect on crop yield, through natural pest control, although Gagic et al. (2017) found little support for this using partly the same data. A lack of consistent relationships between spider activity density and diversity and indicators of land-use intensity has been found before. Li et al. (2018) and Wang et al. (2022) found either negative or positive relationships between spider activity density and nitrogen depending on the composition of the landscape.

Our study found a positive relationship between soil organic carbon content and activity density of non-dominant carabid beetles (Table 3.1, Fig. 3.1c) and a positive trend between SOC content and carabid evenness (Table 3.1). These relationships may be linked as higher SOC content promoted increases in the activity density of non-dominant carabids may have driven an increase in the overall carabid beetle community evenness. We expected that higher soil organic matter content could mitigate the negative effects of increasing land-use intensity and landscape simplification as it can provide additional food resources to what (pests on) crop plants have to offer (Scheu, 2001; Birkhofer et al., 2008). Interactions between the effects of SOC and landscape complexity or land-use intensity were retained in a number of the candidate sets of best models for both carabids and spiders, which suggests that SOC may influence the effect of landscape complexity and land-use intensity. However, support for these interactions was generally low and interaction effects were generally negative. This indicates that differences between fields with contrasting SOC content became smaller with increasing simplification of the landscape or local land-use intensity, which is opposite to our expectation. We found little to no support that SOC content was related to the composition of spider communities which may have to do with SOC providing more valuable resources to the partly herbivorous and omnivorous carabid beetle communities than the strictly carnivorous spider communities. Our study provides modest support that higher SOC content can enhance the activity density and possibly evenness of one important natural enemy group without negatively impacting another important natural enemy group. The relationships between natural enemies and SOC content is comparatively understudied. Because enhancing SOC has other benefits, such as reducing nitrogen leaching and maintaining food production (Tester, 1990; Lal, 2006; Diacono & Montemurro, 2010; Wei et al., 2016), it seems worthwhile to investigate the role of SOC in enhancing natural enemy communities and the services these provide in more detail.

In real-world landscapes, natural communities are generally composed of a few highly abundant species (dominant species) and many rare ones (McGill et al., 2007) and the findings of our study are largely in line with this. Only 9 out of 63 carabid beetle species and 12 out of 71 spider species were identified as nationally dominant species, but they accounted for 90.3% and 91.0% of all collected individuals respectively. Many of the dominant species were dominant in more than one country, which implies that across significant parts of a continent the pest control services are provided by a small number of species. Compared to dominant species, non-dominant species are generally believed to be more vulnerable for agricultural intensification (Purvis et al., 2000; Davies et al., 2004), but we found little support for this. Dominant and non-dominant carabids were related to crop yield and SOC content in similar ways. The only exception was landscape simplicity which showed contrasting relationships between dominant and non-dominant carabid beetle species. However, statistical support for these relationships was poor. Dominant and non-dominant spiders were similarly related to landscape complexity and yield, but relationships with landscape complexity were more pronounced for non-dominant than for dominant species (Table 3.1; Fig. 3.1d, e). The more pronounced effects of landscape complexity on non-dominant spiders may derive from the somewhat different predation strategies of this group compared to the dominant spiders. The ratio of individuals belonging to active hunting spiders or web building spiders was 3.7:1 while in the non-dominant group it was about 1:1 (Table 3.3). The permanent availability of the more complex vertical structure of semi-natural habitats compared to crops could therefore be more important for non-dominant than for dominant spiders. In our study, more than half of the dominant spider species were from the family of Lycosidae (Table 3.3), many species in this family are generally abundant on farmland and robust to on-field management practices and landscape change (Clough et al., 2005; Öberg & Ekbom, 2006; Öberg et al., 2007). An interesting exception was the most dominant web-building spider, i.e., *Pachygnatha degeeri*, the third most often observed spider species across all countries (Table 3.3). Harwood et al. (2005) found that this species relies heavily on aphids, which may explain why wheat crops are suitable habitats for them.

Conclusion

Simultaneously conserving agricultural biodiversity and maintaining crop yield requires us to understand how multiple guilds of natural enemies respond to environmental factors at different spatial scales. Focusing on carabid beetles and spiders, two extremely abundant and widely distributed species groups in agricultural landscapes, we found that they generally respond in contrasting ways to two key indicators of agricultural intensification. Our results provide a better understanding of why measures to enhance natural enemies often do not result in better pest regulation or enhanced crop yield (Chaplin-Kramer et al., 2011; Martin et al., 2013; Tscharntke et al., 2016). The positive relationship between carabid beetles and yield highlights the resilience of some species groups to intensification in agricultural landscapes (although clearly there are boundaries to the level of change communities can absorb without loss of function and service provision; see Deguines et al., 2014; Meehan & Gratton, 2015). This highlights the importance for conservation strategies of distinguishing between species that are well-adapted to anthropogenic landscapes and may actually benefit from modifications to maximize provision of benefits to humans and species that are negatively affected by such changes (Kleijn et al., 2011). A wealth of studies and multiple meta-analyses have focused on how land-use intensity and landscape complexity affect natural enemy diversity and abundance (Chaplin-Kramer et al., 2011; Shackelford et al., 2013; Winqvist et al., 2014; Dainese et al., 2019), but very few studies have examined relationships with soil organic carbon content, which in our study was positively related to components of carabid beetle communities, especially non-dominant species. For arable cropping systems, measures to enhance SOC content deserve more attention as it could potentially represent a management practice that can address multiple benefits to farmers as well as society. In line with the findings for SOC content, our results indicate that restoration of semi-natural habitats will most likely have the strongest positive effects on non-dominant species which generally include the species of conservation concern. Finally, our results suggest that the natural enemy communities providing important pest regulation services are dominated by a small subset of widely distributed species but that non-dominant species do not respond in markedly different ways to the examined potential drivers of biodiversity change than the observed dominant species. Management practices to strengthen populations of endangered farmland species may therefore also enhance service provision by the species group at large, which could be used as an additional argument for conservation. Open that issues remain are what proportion of all species of carabid beetles and spiders utilize farmland habitats and how non-farmland species respond to land-use change related to agricultural intensification.

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Supplementary materials

Table S3.1. Field characteristics (field area, mineral fertilizer and insecticides active substance and applied time during the season) in each country, study region refer to the region sized 100 × 100 km that included all study fields. GE: Germany, NL: the Netherlands, SE: Sweden and UK: the United Kingdom.

Country	Experimental area (m)	Crop grown previous year	Crop growth stage when fertilizer applied	Proportion of cropland within study region	Mean ± SD field area (hectare)	Fertilizer active substance	Total fertilizers active substance (kg/ha)	Insecticide active substance	Insecticide amount (g/ha)	Mean ± SD distance of within-pair separation (km)	Mean ± SD distance of between-pair separation (km)
GE	14×12	Oilseed rape, maize, winter wheat, sugar beet, winter barley	20-25, 29-31, 55-61	49.5%	4.89±4.04	ammonium-sulphate-nitrate	190	beta-Cyfluthrin	7.5	1.25±0.99	11.21±3.75
NL	20×20	sugar beet, potatoes, maize, chicory, peas, flageolet, winter wheat	20+-	62.18%	8.56±5.49	calcium-ammonium-nitrate	170	lambda-cyhalothrin	5	14.09±10.72	18.04±10.10
SE	12.5×26	NA	30	40.52%	22.57±16.99	ammonium nitrate	170	tau-fluvalinate	36	0.43±0.34	12.68±8.46
UK	15×14	Oilseed, beans, Winter wheat	<29, 31-32, 40-50	40.5%	17.26±12.07	ammonium-nitrate	190	deltamethrin	6.25	2.02±1.70	4.98±3.80

Table S3.2. Candidate model set (ΔAICc<2) explaining how soil organic content (SOC), proportion of crop land within 1-km radius (Lcrop), crop yield (Yield) and their interactions on diversity of carabid beetles and spiders. Models are ranked in order of increasing differences in corrected Akaike Information Criterion (ΔAICc). Akaike model weights (ω) indicate the probability that a model is the best approximating model in the candidate set. k indicates the number of parameters in the model. Marginal r^2 (R_m^2) indicates the proportion of variation explained by fixed effects in our model, and conditional r^2 (R_c^2) is the proportion of total variation explained by the model (including variation associated with random factors of field pair and country).

Model No.	SOC	Lcrop	Yield	SOC × Lcrop	SOC × Yield	Lcrop × Yield	k	AICc	ΔAICc	ω	R_m^2	R_c^2
Carabid beetles												
Total activity density												
1							4	556.9	0	0.251	0	0.665
2		0.338					5	557.1	0.22	0.225	0.024	0.685
3	0.690	0.399		-1.339			7	557.2	0.35	0.211	0.086	0.762
4	0.270						5	558.4	1.51	0.117	0.011	0.696
5	0.259	0.338					6	558.8	1.88	0.098	0.036	0.714
6			0.165				5	558.8	1.88	0.098	0.016	0.688
Total species richness												
1	0.189		0.230				5	290.1	0	0.440	0.047	0.624
2			0.219				4	290.6	0.45	0.352	0.032	0.619
3	0.198	-0.100	0.240				6	291.6	1.50	0.209	0.047	0.624
Total evenness												
1	0.044	-0.099		0.212			7	-46.7	0	0.608	0.227	0.360
2	0.112	-0.093					6	-45.8	0.87	0.392	0.167	0.350
Dominant activity density												
1		0.445					5	534.3	0	0.370	0.033	0.743
2							4	534.5	0.16	0.342	0	0.721
3	0.600	0.510		-1.579			7	534.8	0.50	0.288	0.087	0.798
Dominant species richness												
1			0.588				5	183.7	0	0.632	0.038	0.659
2							4	184.8	1.08	0.368	0	0.717

Continued Table S3.2

Model No.	SOC	Lcrop	Yield	SOC × Lcrop	SOC × Yield	Lcrop × Yield	k	AICc	ΔAICc	ω	R_m^2	R_c^2
Non-dominant activity density												
1	0.567						5	355.2	0	0.646	0.064	0.610
2	0.873	-0.056		-0.952			7	356.4	1.20	0.354	0.104	0.579
Non-dominant species richness												
1	0.348		0.247				5	253.6	0	0.270	0.053	0.533
2	0.323						4	253.8	0.24	0.239	0.031	0.535
3	0.366	-0.176	0.268				6	254.8	1.20	0.148	0.070	0.533
4							3	255.1	1.51	0.127	0	0.534
5			0.227				4	255.4	1.79	0.110	0.020	0.536
6	0.336	-0.142					5	255.5	1.85	0.106	0.053	0.533
Spiders												
Total activity density												
1		-0.281	-0.210			-0.777	7	533.1	0	0.360	0.064	0.662
2							4	533.5	0.43	0.291	0	0.645
3			-0.220				5	534.4	1.30	0.187	0.013	0.624
4		-0.206					5	534.7	1.60	0.163	0.011	0.610
Total species richness												
1		-2.621					5	304.0	0	0.492	0.080	0.712
2		-2.665	-0.443			-2.916	7	304.9	0.84	0.322	0.103	0.759
3		-2.633	-0.502				6	306.0	1.95	0.186	0.083	0.714
Total evenness												
1							4	-34.2	0	0.492	0	0.739
2	0.056						5	-33.3	0.84	0.323	0.022	0.757
3	0.107		0.001		0.166		7	-32.2	1.96	0.185	0.071	0.800
Dominant activity density												
1							4	515.7	0	0.438	0	0.565
2			-0.245				5	516.5	0.84	0.287	0.016	0.554
3		-0.180	-0.232			-0.883	7	516.6	0.94	0.274	0.069	0.548

Continued Table S3.2

Model No.	SOC	Lcrop	Yield	SOC × Lcrop	SOC × Yield	Lcrop × Yield	k	AICc	ΔAICc	ω	R_m^2	R_c^2
Dominant species richness												
1		-0.462	-0.462				7	202.2	0	0.249	0.058	0.481
2			-0.436				6	202.6	0.38	0.207	0.027	0.446
3		-0.438					6	202.8	0.58	0.187	0.027	0.446
4							5	202.8	0.62	0.182	0	0.416
5		-0.503	-0.452			-0.802	8	202.9	0.72	0.175	0.078	0.538
Non-dominant activity density												
1		-0.555					5	340.8	0	0.418	0.043	0.704
2		-0.633	-0.062			-0.823	7	341.1	0.28	0.362	0.070	0.784
3	-0.277	-0.603	-0.102			-1.060	8	342.1	1.29	0.220	0.086	0.828
Non-dominant species richness												
1		-0.433					4	250.7	0	1	0.043	0.704

Chapter 4

Distance decay effects predominantly shape spider but not carabid community composition in crop fields in north-western Europe

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Abstract

Agricultural intensification and expansion is regarded as a main driver of biodiversity loss. This conclusion is mainly based on observed declines of local diversity (α-diversity), while effects on community composition homogenization (decrease of β-diversity) at a larger spatial scale is less well understood. Carabid beetles and spiders represent two widespread guilds and are important predators to pest. Here we surveyed carabid beetles and spiders in 66 winter wheat fields in four northwestern European countries (Germany, the Netherlands, Sweden and UK) and analyzed how their community composition was related to geographic distance (separation distance between any pairwise fields) and three environmental variables: crop yield (proxy for land-use intensity), percentage cropland (proxy for landscape complexity) and soil organic carbon content. We further analyzed whether the relationship between carabid beetle and spider community composition and geographic distance was influenced by environmental variables. We found that, 55% and 75% of all observed carabid and spider individuals, respectively, belonged to species that occurred in all four countries. However, individuals of species that were unique to a particular country only accounted for 3% of all collected individuals for both taxa. Furthermore, we found a negative relationship between distance and similarity of spider communities but not for carabid beetle communities. None of the environmental variables were related to similarity of carabid beetle and spider communities, nor moderated the effects of distance. Our study indicates that across a great part of the European continent, arthropod communities (especially carabid beetles) in agricultural landscapes are composed of very similar species that are robust to current variations in environment and land-use.

Key words

β-diversity; biotic homogenization; land-use intensity; landscape complexity; natural enemies; soil organic carbon

Introduction

For centuries, a large proportion of Europe's surface area has been used for a myriad of agricultural production. Historically, a diversity of low-input farming practices created structurally diverse agricultural landscapes that supported numerous species and high levels of biodiversity (Bignal & McCracken, 1996; Henle et al., 2008). However, in response to a combination of the continuously increasing demand for agricultural products and global trade, land-use intensity in agricultural landscapes has increased, with more pesticides and fertilizer being applied to pursue higher yields per unit area and lower costs per unit production. Farming needed to become more efficient, which resulted in larger fields planted with the same crop. This resulted in the loss of semi-natural habitats and has substantially simplified and homogenized agricultural landscapes (Tscharntke et al., 2005). Combined, these changes have resulted in a dramatic loss of biodiversity over recent decades (Kleijn et al., 2009; Emmerson et al., 2016; Maxwell et al., 2016), which is not only problematic from a conservation perspective, but can also jeopardize long-term agricultural productivity as many ecosystem services supported by biodiversity are critical for agricultural production (Zhang et al., 2007).

Arthropod predators like carabid beetles and spiders, which provide pest control services for agriculture, are one of the taxa affected by agricultural intensification. Most research on effects of agricultural intensification and expansion on natural enemy diversity have focused on local-scale diversity (α-diversity). These studies have demonstrated that trends in α-diversity can be driven by a range of on-field agricultural practices like application of fertilizers and insecticides (Hendrickx et al., 2007; Geiger et al., 2010; Li et al., 2018) as well as simplification of the landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Dainese et al., 2019). Recently, more studies have begun to explore the effects of agricultural intensification and expansion on the variation in species composition of arthropod predators among sites (β-diversity, species turnover) (e.g., Hendrickx et al., 2007; Diekötter et al., 2010). However, these studies have only examined how community composition of a single taxon responds to a single practice of agricultural intensification or agricultural landscape simplification (Ekroos et al., 2010; Inclán et al., 2015; Rusch et al., 2016a). Although these studies have provided valuable insights, we still know much less about how community composition of different taxa respond to environmental factors at multi-spatial scales. Beta-diversity is an important component of biodiversity that is influenced at larger spatial scales (Socolar et al., 2016), therefore β-diversity is invariably related to separation distance because the distribution of organisms is inherently determined by two processes: the adaptation of species to the local environmental conditions and dispersal limitation (Hubbell 2001; Tuomisto et al., 2003). With increasing distance, the environmental conditions will become less similar from the local environmental conditions and these places will be more difficult to disperse to. This leads to a typical decrease in similarity (or increase in β-diversity) between communities that are located further apart (distance decay effects, Soininen et al., 2007). However, it has been rarely examined whether for natural enemies such patterns will be affected by environmental or management factors. For plant communities, Buhk et al. (2017) found that β-diversity was lower in intensively managed agricultural landscapes than in low-intensity landscapes because in the intensively managed landscapes plant communities from different regions only contained species that were generalists or good dispersers.

The same could apply to natural enemies. Not all species will respond in the same way to increasing land-use intensity or landscape simplification (Gámez-Virués et al., 2015; Simons et al., 2016). Rare or specialist species are more vulnerable to agricultural intensification and disappear more rapidly (Davies et al., 2004; Öckinger et al., 2010), while generalist species are more robust and persist or even increase (Flohre et al., 2011; Kleijn et al., 2015). This, across large areas, could result in arthropod communities that inhabit intensive agricultural landscapes becoming composed of the same generalist species or species with similar functional traits, thereby driving the biotic homogenization of agricultural farmlands (McKinney & Lockwood, 1999; Gámez-Virués et al., 2015; Ponisio et al., 2015). Furthermore, ground-dwelling natural enemy community composition can also be affected by local soil characteristics. Soil with a higher organic matter content provides resources for a larger soil food web potentially accommodating larger numbers of top predators such as natural enemies (Bulluck et al., 2002; Birkhofer et al., 2008). In theory, this could allow more rare and endemic species to persist in sites with higher soil organic matter content regardless of land use intensity or landscape simplification, resulting in more heterogeneous communities between sites. However, studies that have to date examined the effects of soil organic matter on natural enemy communities have produced contrasting results. It has been found that higher soil organic matter supported more diverse and even carabid and spider communities and such effects were greater on non-dominant species (Gagic et al., 2017; Aldebron et al., 2020; Kolb et al., 2020). In contrast, Hadjicharalampous et al. (2002) found that the abundance of dominant arthropod species groups was positively related with soil organic matter while this relationship was negative for rare and uniquely distributed species groups. In sum, there is still no consensus about how soil organic matter content influences α-diversity of natural enemies and we have only scratched the surface of the relationship between soil organic matter content and β-diversity.

Here we collected data on carabid beetle and spider communities in 66 paired winter wheat fields contrasting in soil organic carbon content in four north-western European countries (Germany, the Netherlands, Sweden and United Kingdom), and quantified landscape composition, local land-use intensity and soil organic matter content for each site. We aimed to understand how β-diversity of carabid beetles and spiders responds to geographic distance and local and landscape environmental variables. Specifically, we asked (1) whether and how the β-diversity of carabid beetle and spider communities is related to geographic distance, landscape composition, land-use intensity and soil organic carbon content and (2) whether and how the relationship between β-diversity and geographic distance was influenced by any of the considered environmental variables.

Method

Study design

In 2014, we selected eight pairs of conventionally managed winter wheat fields in the Netherlands, Sweden and the United Kingdom and nine pairs in Germany, resulting in a total of 33 pairs of fields. These paired fields were a subset of the fields used by Gagic et al. (2017). The two fields within each pair had contrasting soil organic matter content resulting from different management histories such as the application of mineral fertilizers, manure, crop rotation or tillage practices but were otherwise as similar as possible with respect to landscape complexity and soil conditions (e.g., soil pH and texture). In Germany, Sweden and the United Kingdom, each field was always closer to its paired field than to fields in other pairs (Table S4.1). Due to high soil variability in the Netherlands, it was not always possible to pair nearby fields with matching soil type and local landscape context so that here similar fields were not paired spatially but were all located in a single study region.

To validate whether fields within each pair had contrasting soil organic matter content but the same soil type and similar pH (i.e., a difference of no more than 0.5), we collected five soil samples at each field. These soil samples were collected before the first fertilizer application at a distance of 5-8 m from the crop edge and were pooled and mixed before analysis. Soil organic carbon (SOC) content was measured as the proxy for soil organic matter content. SOC content was assessed via the loss on ignition method (Hoogsteen et al., 2015). This showed that differences between paired high and low SOC content fields turned out to be relatively small and some low SOC fields were found to actually have higher SOC content than a high SOC content field in another pair. We therefore decided to use SOC content as a continuous variable in the statistical analyses instead of a categorical one (high or low). Within each region, field pairs were chosen across a gradient in landscape complexity, which was calculated as the percentage of cropland within a 1-km radius around each study field. The percentage cropland is often used as a proxy for landscape complexity and is generally negatively related to the proportion of semi-natural area and habitat diversity in the landscape (Rusch et al., 2016b; Martin et al., 2019).

The original study of Gagic et al. (2017) was designed to experimentally examine the impacts of fertilizer and pesticide applications. These experimental treatments are not being used in the current study, but to understand how the data were obtained we briefly describe the experimental design here. In each field, a plot with a minimum size of 56 × 12 m was set up with the longer side adjacent to the field boundary and at least 10 m away from the nearest field corner. The field boundary characteristics were matched as far as possible within each pair. Each plot was divided into four equally sized treatment subplots to which randomly allocated fully crossed insecticide and mineral fertilizer applications (present vs absent) were assigned. The insecticides were locally recommended types of pyrethroids (broad spectrum) and the fertilizers were ammonium nitrate based and both were applied by project members following regionally recommended rates and frequency. Insecticides were applied regardless of pest outbreaks and farmers were allowed to use herbicides and fungicides in the treatment plots.

In each treatment subplot, we selected squares sized 0.25 m^2 (a total of 1 m^2 for each field) and manually harvested the wheat. The harvested wheat ears were air dried to approximately 14% moisture content, threshed and then weighted expressed as grain dry weight per hectare (t/ha). We used wheat yield as a proxy for local land-use intensity, which is often done (Dietrich et al., 2012; Gabriel et al., 2013; Winqvist et al., 2014), as it represents the end result of all short- and long-term management practices.

Surveying ground-dwelling arthropods

Pitfall traps (polypropylene beakers 155 mm high and 95 mm across) were used to survey ground-dwelling arthropods during the wheat flowering season (late May to early June). We placed one pitfall trap in the center of each treatment subplot at least 10 m from the field boundary and filled it with 200 mL of a mixed solution of 2/3 water and 1/3 glycol and a drop of detergent to lower surface tension. A square aluminium plate was placed *c.* 10 cm above each pitfall trap to prevent flooding by rain. Pitfall traps were opened for a period of 10 days after which all arthropods were collected and stored in 70% ethanol solution for later identification. From all arthropods, we selected the two most abundant species groups, carabid beetles (Carabidae) and adult spiders (Araneae) as our bioindicators and they were counted and identified to species level using standard keys (Hackston, 2020; Nentwig et al., 2021).

Data analysis

All statistical analyses were conducted in R version 4.2.1 (R Core Team, 2022b).

Response variables

Because in this study we were interested in factors explaining similarities in species composition between fields, and not in the subplot-scale effects of the different experimental treatments (which had already been examined by Gagic et al., 2017), we pooled the collected carabid beetles and spiders over the different treatments. Because each field had been subjected to the same combination of treatments and earlier analyses showed that the effects of these treatments on carabid beetle and spider abundance were generally not influenced by the environmental variables (Appendix 3 of Gagic et al., 2017), pooling the samples should not affect the relationships of the environmental variables across fields. Our sampling intensity was the same in all fields which made the community composition across all possible pair-wise combinations of all fields comparable (Schroeder & Jenkins, 2018). Abundance-based Bray–Curtis dissimilarity index was calculated (using “vegan” package; Oksanen et al. 2022) as the Bray-Curtis index incorporates information about the relative abundance of each species in addition to the occurrence of species and is recommended when composition and relative abundance data are available (Chao et al. 2006; Anderson et al. 2011). Our data represent activity-density data, but because all of our fields were wheat fields, the vegetation structure was very similar which is why we consider it a reliable proxy for abundance. The Bray-Curtis index ranges from 0 (two communities with the same species and each species with the same abundance) to 1 (two communities with no species in common). Since using similarity would be more intuitive, we used 1 minus Bray–Curtis index for each group as our response variable.

Explanatory variables

The environmental variables SOC content, wheat yield and percentage cropland in a 1 km buffer were included as explanatory variables. For each possible field-pair combination and environmental variable, we calculated and included in the analyses both the difference in environmental variables between pairs of fields and the mean of the two fields that were compared. The difference provides an indication of the contrast in environmental conditions, while the mean gives an indication of the overall conditions in the two fields (Gossner et al., 2016). Additionally, the geographic distances between all possible combinations of pair-wise compared fields were included as an explanatory variable, calculated using the “geodist” package (Padgham & Sumner, 2022). Thus, seven variables were included as explanatory variables in our study.

Statistical analysis

Fields with missing data for environmental variables, carabid beetle or spider data were omitted from the analyses resulting in a total of 57 and 56 fields for carabid beetles and spiders, respectively. Simply making all-possible combinations of pairwise comparisons between all fields would result in pseudo-replication. We therefore used a randomization procedure. We first randomly divided fields into two equal subsets of 28 fields each and then randomly paired fields between the two subsets resulting in 28 pairwise community similarity comparisons for both species groups. This randomization procedure was repeated to generate 10,000 datasets that make independent comparisons of carabid beetles and spiders respectively, which were then used in all following analysis.

Distance generally plays an important role in influencing community similarity but it is less clear what distance function best explains community similarity (Nekola & White, 1999; Tuomisto et al., 2003; Ferenc et al., 2013). We therefore first used linear regression models to examine which of four distance functions (linear distance, ln-transformed distance, square-root transformed distanced and quadratic polynomial transformed distance) best explained the community similarity of carabid beetles and spiders respectively. In these analyses, for all distance functions the calculated distances between paired fields from the 10,000 datasets were standardized using the R package "standardize" (Eager, 2021). We compared the output of the models using different distance functions using the Akaike Information Criterion values corrected for small sample size (AICc) using R package MuMIn (Bartoń, 2022) and then ranked the models based on the average AICc value across the analyses of the 10,000 datasets. For both carabid beetles and spiders, ln-transformed distance was the best predictor (Table S4.2) which was therefore used in all subsequent analyses.

The core analyses used multiple linear regression models to examine how ln-transformed distance and (combinations of) different environmental variables influence community similarity of carabids and spiders. For each of the 28 pairwise fields in all 10,000 datasets we calculated the difference and mean values of the environmental variables, which were then standardized within each dataset (using the R package "standardize"; Eager, 2021). We constructed one intercept-only model, seven models each with a single explanatory variable (only distance or difference or mean of environmental variables), six models each including distance and one of the difference or mean of environmental variables as explanatory variables, and six models each including interactions of distance and one of the six environmental variables as explanatory variables, thus resulting in a total of 20 models (Table S4.3). For each model we calculated mean AICc values based on analysis of all the 10,000 datasets, ranked the different models based on the average AICc values and then calculated full-model averaged parameter estimates and confidence intervals based on all models with Δ average AICc < 6 (Table S4.3).

Results

Overall, we collected 3284 carabid beetles belonging to 63 species and 2730 adult spiders belonging to 71 species and 15 families. Five carabid beetle species and eight spider species were observed in all four countries and the relative abundance of these species were 55.4% and 74.9% respectively. There were 13 carabid beetle species and 24 spider species only observed in Germany with relative abundance of 1.19% and 1.79% respectively. These numbers were 5 and 3 (0.27% and 0.21%) for the Netherlands, 16 and 15 (1.47% and 1.32%) for Sweden and 8 and 2 (0.37% and 0.07%) for the United Kingdom (Fig. 4.1).

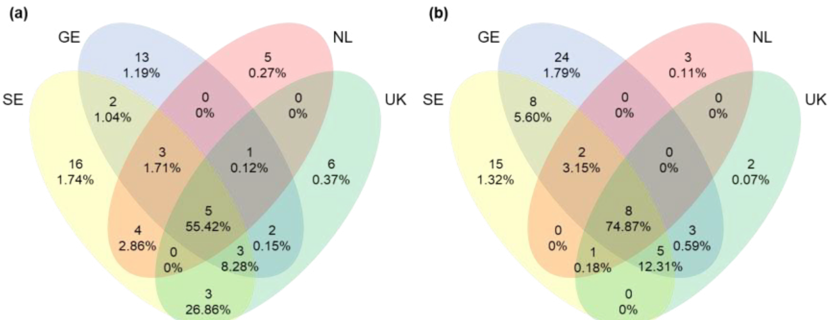

Fig. 4.1. Venn diagrams of observed (a) carabid beetle and (b) spider species in four countries (GE, Germany; NL, the Netherlands; SE, Sweden; UK, the United Kingdom). Top numbers indicate the species number that are shared by multi countries or exclusive in one country, bottom numbers with percent sign indicate the relative abundance of the corresponding shared or exclusive species.

Table 4.1. Model averaged results for distance and environmental variables explaining community composition similarity of carabid beetles and spiders. Since ln-transformed distance was found to be the best model than other types of distance for both carabid beetles and spiders (Table S4.2), "distance" in this table indicates ln-transformed distance. * Indicates the interaction between distance and environmental variables. Predictors with a 95% confidence interval that did not overlap 0 are shown in bold. Models were averaged based on the candidate set of best models (Δ average AICc < 6 in Table S4.3). Results are based on 10,000 iterations.

Guild	Predictor	Mean Coefficient	Mean adjusted SE	95% confidence interval
Carabid	**Distance**	**-0.0374**	**0.1808**	**-0.0561 to -0.0186**
	Lcrop Mean	-0.0028	0.1211	-0.0153 to 0.0098
	SOC Mean	-0.0001	0.1136	-0.0119 to 0.0117
	Yield Mean	0.0038	0.1216	-0.0088 to 0.0164
	Lcrop Difference	0.0012	0.1204	-0.0113 to 0.0137
	SOC Difference	0.00002	0.1191	-0.0123 to 0.0124
	Yield Difference	-0.0017	0.1218	-0.0143 to 0.0110
	Distance * Lcrop Mean	-0.0003	0.0922	-0.0099 to 0.0092
	Distance * SOC Mean	-0.0004	0.0841	-0.0092 to 0.0083
	Distance * Yield Mean	-0.00006	0.0910	-0.0095 to 0.0094
	Distance * Lcrop Difference	0.0008	0.0946	-0.0090 to 0.0106
	Distance * SOC Difference	-0.0008	0.1029	-0.0115 to 0.0098
	Distance * Yield Difference	0.0011	0.0993	-0.0092 to 0.0114
Spider	**Distance**	**-0.0971**	**0.1811**	**-0.1159 to -0.0783**
	Lcrop Mean	-0.0017	0.1058	-0.0126 to 0.0093
	SOC Mean	0.0070	0.1244	-0.0059 to 0.0199
	Yield Mean	0.0050	0.1166	-0.0071 to 0.0171
	Lcrop Difference	-0.0013	0.1082	-0.0125 to 0.0100
	SOC Difference	0.0086	0.1330	-0.0052 to 0.0224
	Yield Difference	0.0051	0.1177	-0.0072 to 0.0173
	Distance * Lcrop Mean	0.0004	0.0968	-0.0097 to 0.0104
	Distance * SOC Mean	-0.0003	0.0964	-0.0103 to 0.0097
	Distance * Yield Mean	0.0010	0.1005	-0.0094 to 0.0115
	Distance * Lcrop Difference	-0.0004	0.1021	-0.0110 to 0.0103
	Distance * SOC Difference	-0.0029	0.1232	-0.0157 to 0.0098
	Distance * Yield Difference	-0.0004	0.1075	-0.0116 to 0.0107

For spiders, distance played an important role in shaping community similarity. The model with only distance as explanatory variable was the most highly ranked model (Table S4.3) and the confidence interval of the mean coefficient did not overlap zero (Table 4.1). This suggests that between sites the similarity in community composition for spiders was strongly negatively related with distance (Fig. 4.2). Although for carabid beetles the model with only distance as explanatory variable was also the most highly ranked model, here the intercept-only model was included in the candidate set of best models (second best model at Δ AICc = 1.42; Table S4.3). This indicates that the model with only distance as an explanatory variable did not perform meaningfully better than a model without any explanatory variable. The difference in relationship between community composition and distance between the two species groups was further highlighted by the mean coefficients which was almost three times steeper for spiders than for carabids (-0.0372 vs -0.0976, Fig. 4.2). Interestingly, there was no support for any of the environmental variables being strongly related with between-sites similarity in carabid beetle or spider communities: coefficients of all environmental variables were low and confidence intervals overlapped zero without exception (Table 4.1). Furthermore, we found no support for these variables moderating the relationship with distance as none of the interactions between environmental variables and distance had high mean coefficients and all confidence intervals overlapped zero (Table S4.3).

Discussion

We found support for a negative relationship between distance and similarity of spider communities but not for carabid beetle communities. Furthermore, we found no support for any of our investigated environmental variables being related to between-field community similarity, nor for them moderating the relationship with distance. The lack in differentiation in natural enemy communities in response to environmental variables may have been caused by communities from both guilds being dominated by individuals from species that are widespread in north-western Europe, with 55% and 75% of the total number of the observed carabid and spider individuals, respectively, belonging to species that occurred in all four countries (Fig. 4.1). Although approximately two-thirds of the total number of species of both groups were observed in a single country, the total relative abundance of these species was very low (only 3% for both groups).

In line with previous studies (Soininen et al., 2007; Keil et al., 2012; Boieiro et al., 2013; Zhang et al., 2013), we found that distance played a predominant role in shaping community β-diversity for spiders. This pattern was not caused by spider communities in nearby sites being consistently similar. Rather, spider communities in fields that were far apart were consistently dissimilar and communities from nearby fields showed the entire range from being similar to dissimilar (Fig. 4.2). This shows that two communities close to one another are not necessarily similar (Arribas et al., 2021), but on average nearby communities are more similar than communities that are far apart. Furthermore, we found that β-diversity of spiders (and carabid beetles) was best explained by ln-transformed distance. This suggests that the relationship between distance and community similarity was not linear but showed the most pronounced change at smaller distances and changed relatively less at greater distances (Condit et al., 2002; Tuomisto et al., 2003).

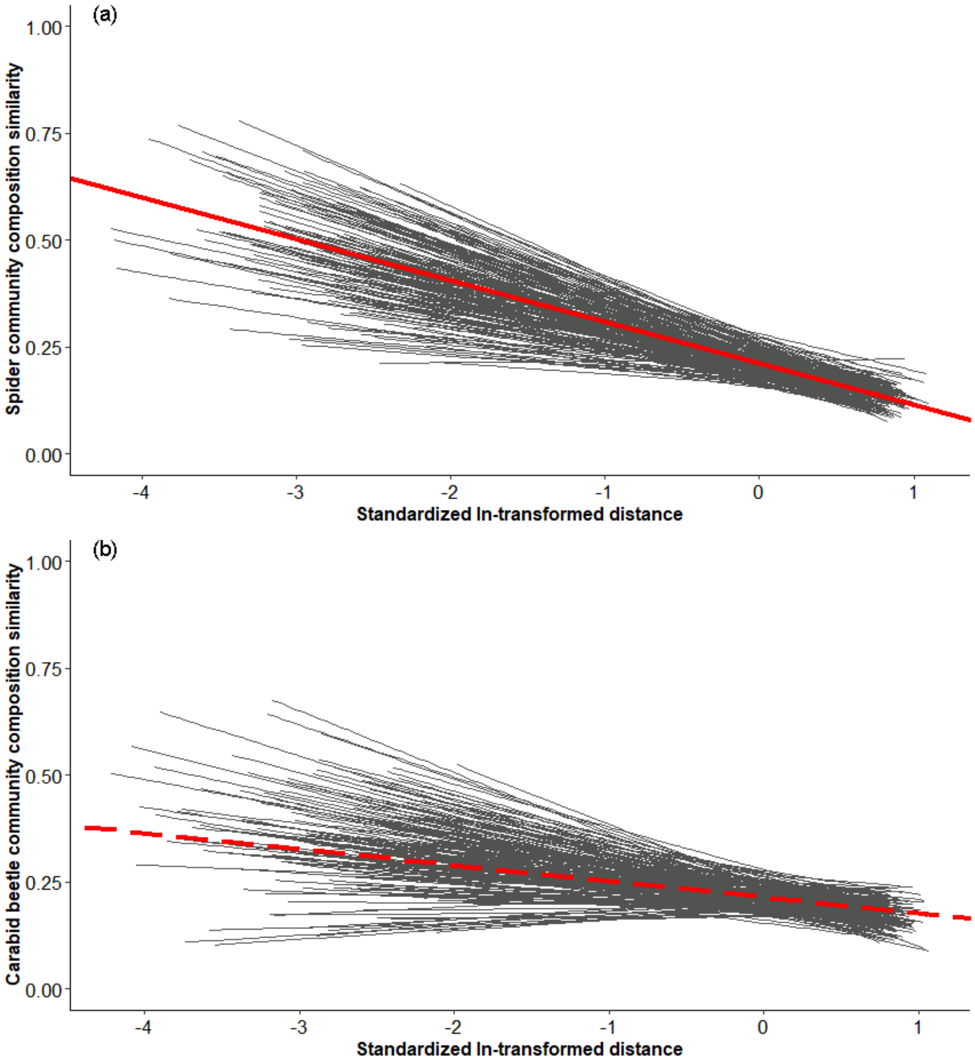

Fig. 4.2. A visualization of the relationships between standardized ln-transformed distance and community composition similarity of spiders (a) and carabid beetles (b). Gray lines indicate regression lines calculated from 200 randomly selected dataset, red line indicates averaged regression line of the overall 10,000 randomized datasets.

Interestingly we found no convincing support for any explanatory variable explaining the similarity of carabid beetles between fields. One reason could be that the level of endemism of the observed species in our study was much lower for carabid beetles than for spiders. While some spider species were found to be exclusively distributed in Germany and Sweden, none of the carabid beetle species were found to be uniquely distributed in any of these four countries (Schuldt & Assmann, 2009 & 2010). This potentially suggests higher species nestedness for spiders than for carabid beetles which may have resulted in a stronger distance decay effects on spider assemblages. For carabid beetles the lack of any meaningful relation with distance suggests that wheat fields in Sweden harboured essentially the same carabid beetle communities as wheat fields in Germany or the UK which are ~1000 km apart.

In general, the similarity of environmental conditions will decrease with increasing distance between two sites, which is supposed to drive the main effects determining distance decay effects (Tuomisto et al., 2003). However, in arable fields farmers attempt to minimize variation and eliminate factors constraining agricultural production. In northwestern Europe, virtually all arable fields are therefore nutrient-rich, well-drained and mostly free of any plant species that is not the crop. In our study we furthermore only sampled a single crop type making the studied fields even more similar. The increasing contrast in environmental conditions between two sites, that may be expected to occur with increasing distance under natural conditions, may therefore be much less pronounced in the examined arable fields. This could explain why our study, in line with results of earlier studies, did not find land-use intensity, landscape complexity and soil organic carbon content to affect the beta-diversity of both carabid beetles or spiders (Hendrickx et al., 2007; Diekötter et al., 2010; Gossner et al., 2016; Lafage & Pétillon, 2016). The relationship between distance and community similarity for spiders could then be caused by the fact that in this study system, activity density and species richness of spiders are more strongly linked to semi-natural habitats than carabid beetles (Mei et al. 2023). The fact that the collected arthropod communities in our study were dominated by a few species and that these species were found across a significant part of the European continent suggests that these are the species that are well adapted to the conditions of arable fields, these species are robust to environmental differences and that they can persist during environmental change (Desender et al., 2010; Rusch et al., 2013b; Gámez-Virués et al., 2015). Therefore, from a utilitarian perspective, our results suggest that similar practices to enhance natural pest control service can be implemented across different countries as these countries share very similar arthropod predator communities.

The results of our study suggests that, while many species may have gone locally extinct because of agricultural intensification and the associated management practices, a few species have most likely been favoured by the environmental conditions now available in modern agricultural landscapes, allowing them to dominate communities across large geographical regions. These species can be regarded as "winner species" (McKinney & Lockwood, 1999), which help guarantee the resilience of natural enemy communities in agricultural landscapes and are the key providers of important ecosystem services (Kleijn et al., 2015; Winfree et al., 2015). However, these “winner species” were estimated to only account for about 1% of the total number of species (McKinney & Lockwood, 1999). If the trend of agricultural expansion and intensification continues, it will cause severe extinction of specialist and endemic species and drive biotic homogenization in agricultural landscapes (McKinney & Lockwood, 1999; Karp et al., 2012). Since the gain of these “winner species” even may outweigh the loss of the “loser species” and can result in the net increase of species richness (Finderup Nielsen et al., 2019), only focusing on α-diversity may bias the assessment of the status and trends of biodiversity in agricultural landscapes. Our study highlights that biotic homogenization could be a more substantial consequence than local diversity loss under agricultural intensification. Therefore, the first step of biodiversity conservation should distinguish between the “winner species” and “loser species”, followed by more specific conservation measures targeting these “loser species” to create or restore the resources that match the need of these species.

Acknowledgments

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Supplementary materials

Table S4.1. Field characteristics (field area, mineral fertilizer and insecticides active substance and applied time during the season) in each country, study region refer to the region sized 100 × 100 km that included all study fields. GE: Germany, NL: the Netherlands, SE: Sweden and UK: the United Kingdom.

Country	Experimental area (m)	Crop grown previous year	Crop growth stage when fertilizer applied	Proportion of cropland within study region	Mean ± SD field area (hectare)	Fertilizer active substance	Total fertilizers active substance (kg/ha)	Insecticide active substance	Insecticide amount (g/ha)	Mean ± SD distance of within-pair separation (km)	Mean ± SD distance of between-pair separation (km)
GE	14×12	Oilseed rape, maize, winter wheat, sugar beet, winter barley	20-25, 29-31, 55-61	49.5%	4.89±4.04	ammonium-sulphate-nitrate	190	beta-Cyfluthrin	7.5	1.25±0.99	11.21±3.75
NL	20×20	sugar beet, potatoes, maize, chicory, peas, flageolet, winter wheat	20+-	62.18%	8.56±5.49	calcium-ammonium-nitrate	170	lambda-cyhalothrin	5	14.09±10.72	18.04±10.10
SE	12.5×26	NA	30	40.52%	22.57±16.99	ammonium nitrate	170	tau-fluvalinate	36	0.43±0.34	12.68±8.46
UK	15×14	Oilseed, beans, Winter wheat	<29, 31-32, 40-50	40.5%	17.26±12.07	ammonium-nitrate	190	deltamethrin	6.25	2.02±1.70	4.98±3.80

Table S4.2. Model selection table showing results for relationships between different types of distance functions and community composition similarity of carabid beetles and spiders. Models are ranked with increasing Δ average AICc values. Results are based on 10,000 iterations.

Guild	Types of distance	Average AICc	Δ average AICc
Carabid	ln-transformed distance	-21.43	0
	square-rooted distance	-20.38	1.05
	quadratic polynomial transformed distance	-19.69	1.74
	original distance	-19.48	1.95
Spider	ln-transformed distance	-26.41	0
	square-rooted distance	-25.04	1.37
	quadratic polynomial transformed distance	-23.68	2.73
	original distance	-22.79	3.62

Table S4.3. Model selection table showing results for relationships between environmental variables and distance and community composition similarity of carabid beetles and spiders. Since ln-transformed distance was found to be the best model for both carabid beetles and spiders (Table S2), "distance" in this table indicates ln-transformed distance. + indicates separate distance and environmental variables and * indicates interaction between distance and environmental variables. Models are ranked with increasing Δ average AICc values. Results are based on 10,000 iterations.

Models	Average AICc	Δ average AICc
Carabid beetles		
Distance	-21.43	0
(Intercept)	-20.01	1.42
Distance + Yield Mean	-19.83	1.60
Distance + Lcrop Mean	-19.79	1.64
Distance + Lcrop Difference	-19.78	1.65
Distance + Yield Difference	-19.76	1.67
Distance + SOC Mean	-19.50	1.93
Distance + SOC Difference	-19.48	1.95
Yield Mean	-18.60	2.83
Lcrop Mean	-18.57	2.86
Yield Difference	-18.56	2.87
Lcrop Difference	-18.48	2.95
SOC Difference	-18.36	3.07
SOC Mean	-18.31	3.12
Distance * Lcrop Mean	-18.17	3.26
Distance * Yield Mean	-18.15	3.28
Distance * Lcrop Difference	-18.14	3.29
Distance * Yield Difference	-18.13	3.30
Distance * SOC Difference	-17.73	3.70
Distance * SOC Mean	-17.70	3.73
Spiders		
Distance	-26.41	0
Distance + SOC Mean	-25.73	0.68
Distance + SOC Difference	-25.67	0.74
Distance + Yield Mean	-25.27	1.14
Distance + Yield Difference	-25.19	1.22
Distance + Lcrop Difference	-24.75	1.66
Distance + Lcrop Mean	-24.68	1.73
Distance * SOC Difference	-24.48	1.93
Distance * SOC Mean	-24.28	2.13

Continued Table S4.3

Models	Average AICc	Δ average AICc
Distance * Yield Mean	-23.97	2.44
Distance * Yield Difference	-23.85	2.56
Distance * Lcrop Difference	-23.65	2.76
Distance * Lcrop Mean	-23.46	2.95
(Intercept)	-17.55	8.86
SOC Mean	-16.59	9.82
Yield Mean	-16.53	9.88
Lcrop Difference	-16.13	10.28
Yield Difference	-16.13	10.28
Lcrop Mean	-16.07	10.34
SOC Difference	-15.92	10.49

Chapter 5

Arthropod predator identity and evenness jointly shape delivery of pest control services

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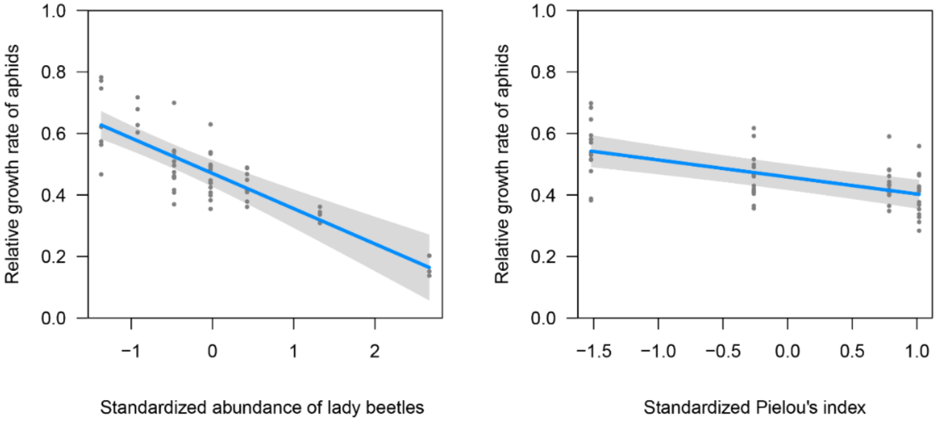
Abstract

Background: Maximising the effectiveness of natural pest control requires a detailed understanding of how service delivery is affected by natural enemy community diversity and composition. Many studies have investigated the effects of natural enemy abundance and species richness on pest control. Studies examining the effects of evenness and species identity are fewer and have produced inconsistent results. Here we test the effects of arthropod predator community evenness and species identity on natural pest control by exposing aphid (*Sitobion avenae*) colonies in experimental cages to arthropod predator communities that had the same abundance and species richness but that differed in evenness and dominant species.

Results: We found that the identity of the most dominant species in the arthropod predator community predominantly drove the pest control efficiency. However, additional to the effects of species identity, we also found a causal positive relationship between the evenness of arthropod predator communities and the suppression of pest growth.

Conclusion: Our results provide support for the hypothesis that ecosystem service provision is generally a function of abundance and efficiency of the most dominant species of the service providing groups. This could partly explain why management practices aiming at promoting abundance of natural enemies often have mixed effects on pest control. Our results also demonstrate that diversity components such as evenness have important additional effects. However, in real world ecosystems these effects may be obscured because evenness is generally confounded with abundance or species richness in natural enemy predator communities.

Graphic abstract



Studies investigating how natural enemy evenness and identity affect pest control efficiency are rare and have produced inconsistent results. Using experimental natural enemy communities under strictly controlled conditions, we found that pest control efficiency was predominantly determined by the abundance of the most efficient species but was additionally enhanced by the evenness of the natural enemy communities.

Key words

cage experiment; *Coccinella septempunctata*; community composition; dominant species; natural enemy; *Sitobion avenae*

Introduction

Agriculture relies heavily on ecosystem services provided by multiple guilds of service-providing species (Bianchi et al., 2006; Losey & Vaughan, 2006; Aizen & Harder, 2009; Gallai et al., 2009). In recent decades, agricultural management aimed to enhance productivity has resulted in significant loss of species that regulate key processes underlying agricultural production (Matson et al., 1997; Chapin et al., 2000). Crop yield and quality often no longer respond to additional agricultural inputs because ecosystem service-providing species have become the limiting factor (Classen et al., 2014; Fijen et al., 2020). A wealth of studies examining the biodiversity-ecosystem functioning relationship show that service provision increases with species richness of service-providing communities (Griffin et al., 2013; Jonsson et al., 2017; Dainese et al., 2019). This implies that restoration management should target on species richness (Dainese et al., 2019). At the same time, species communities in agricultural landscapes are generally dominated by a few generalist species (Kleijn et al., 2015; Mei et al., 2023) and service provision is mainly determined by the abundance of a small subset of dominant species (Winfree et al., 2015). This could indicate that service provision can be safeguarded by enhancing the abundance of a few easily manageable species (Kleijn et al., 2015). However, these two observations are not mutually exclusive, because service-providing species communities that have a more even distribution of species could still outperform communities of the same richness that are heavily dominated by one or a few species. While species-richness effects on ecosystem service provision have been examined extensively (reviewed by van der Plas, 2019), we know much less about the effects of dominance and evenness on service provision (Hillebrand et al., 2008; Wittebolle et al., 2009; Snyder, 2019).

Pest control provided by natural enemies is one of the most important regulating services that can reduce the reliance of agricultural production on pesticides (Bommarco et al., 2013). Many studies show that higher abundance or species richness of natural enemies provide higher pest suppression rate (Griffin et al., 2013; Jonsson et al., 2017; Dainese et al., 2019). This is because larger numbers of natural enemies consume more pest food resources and because more species-rich natural enemy communities deploy a wider range of predation strategies with different species complementing each other (Finke & Snyder, 2008; Snyder, 2019). However, the evidence base for effects of the evenness of natural enemy communities on pest control is much smaller (Snyder, 2019) and the few studies to date that have addressed the topic have demonstrated positive (Crowder et al., 2010; Mace & Mill, 2017; Yuan et al., 2019), neutral (Rusch et al., 2015; Mace & Mills, 2017; Riggi et al., 2017) and even negative (Dainese et al., 2019) effects of higher natural enemy evenness on delivery of natural pest control service.

The conflicting results could be explained by the effects of species identity. It has been suggested that the efficiency of a community to provide ecosystem services is determined by the proportion of the species that most efficiently provide the ecosystem services (Hillebrand et al., 2008). If higher evenness is achieved by lowering the relative abundance of the most efficient species this will reduce service provision. However, if it is achieved through lowering the relative abundance of a less efficient species this may increase service provision (Crowder & Jabbour, 2014). An additional complicating factor in the case of pest control is that natural enemies not only prey on pest species but may also predate one another (Finke & Denno, 2003). Such intraguild predation, or interference effects, may strongly affect the outcome of studies examining species richness effects on pest control because outcomes will depend on the exact combination of species regardless of richness or evenness (Snyder et al., 2022). Species identity has been found to have a larger impact on pest control than species richness (Straub & Snyder, 2006; Rizali et al., 2018), but evenness has been found to contribute to pest control independently from species identity effects (Crowder et al., 2010). Which mechanisms explain the effects of evenness on pest control is not well understood (Snyder, 2019). The mechanisms are probably similar to the ones underlying predator richness effects; positive complementarity effects that are counteracted by negative effects of enemy interference (Crowder et al., 2010; Crowder et al., 2012). Given the potential importance of evenness on provision of pest control services, it is important to develop a better understanding of its effects and underlying mechanisms.

Here, we examine the effects of arthropod predator evenness and identity on aphid predation efficiency by using a model system with the aphid species *Sitobion avenae* on wheat (*Triticum aestivum*). We selected four species of natural enemies that prey on *S. avenae* belonging to different guilds: two flying species (the lady beetle *Coccinella septempunctata* and the mirid bug *Macrolophus pygmaeus*) and two ground-dwelling species (the carabid beetle *Poecilus cupreus* and the spider *Trochosa ruricola*). We introduced aphids on wheat plants in large experimental cages which were then exposed to five treatments; one control treatment with no arthropod predators and four treatments with different combinations of the arthropod predators that all had the same abundance and species richness but different evenness. These cages created confined environments to guarantee that aphids were only exposed to the experimental arthropod predator communities or the control situation without predators. We specifically asked whether and to what extent 1) the evenness of the arthropod predator communities and 2) the abundance of individual species affect aphid population growth rate.

Materials and method

System design and species selection

Wheat (*Triticum aestivum*) as an important food crop is often severely damaged by many pests, among which, *Sitobion avenae* represents the most dominant and harmful one (Vickerman & Wratten, 1979). It can cause substantial wheat yield loss with as few as 4 aphids per straw (Larsson, 2005) and its risky areas are predicted to constantly expand globally (Wang et al., 2023). *S. avenae* has a wide range of natural enemies including predators and parasites. In this study, we selected four species of arthropod predators (two flying species: the lady beetle *Coccinella septempunctata* and the mirid bug *Macrolophus pygmaeus*, and two ground-dwelling species: the carabid beetle *Poecilus cupreus* and the spider *Trochosa ruricola*) as the natural enemies of *S. avenae*. These species are native and dominant species in the Netherlands which made them easier to purchase online or collect. *C. septempunctata* has been regarded as one of the most efficient predators on aphids (Straub & Snyder, 2006; Long & Finke, 2014) which has been shown to play a key role in suppressing *S. avenae* in wheat fields (Rana, 2005). *M. pygmaeus* as a polyphagous predator can consume multiple pests including aphids, whiteflies, mites and thrips (Weintraub et al., 2017). Furthermore, *M. pygmaeus* is commonly found in agroecosystems and can persist under a wide temperature range even without prey (Perdikis & Lykouressis, 2000). Therefore, *M. pygmaeus* is frequently used as biocontrol agent in practical agricultural production (Weintraub et al., 2017). Besides the two flying arthropod predators, ground-dwelling arthropod predators like carabid beetles and spiders can also predate on aphids, and the effectiveness of ground-dwelling natural enemies in suppressing aphids has even been reported to outperform flying ones in some cases (Caballero-López et al., 2012). *P. cupreus* and *T. ruricola* are the most dominant ground-dwelling arthropod predator species in the Netherlands (Mei et al., 2023). Both these species can predate on *S. avenae* (von Berg et al., 2012), with *T. ruricola* displaying a strong preference for *S. avenae* (von Berg et al., 2012).

Experimental design

The experiment was carried out at the experimental farm of Wageningen University & Research from 15 June to 2 October in 2021 (51°59'47" N, 5°39'36" E, Wageningen, the Netherlands). The objective of the experiment was to examine how natural enemy assemblages with different evenness but the same species richness and abundance affect the efficiency of pest predation. To this end, we used the aphid pest species *S. avenae* on wheat (*T. aestivum*) exposed to four species of arthropod predatory natural enemies (*C. septempunctata*, *M. pygmaeus*, *P. cupreus* and *T. ruricola*) as our model system. To exclude as much as possible any external interference with the experimental arthropod communities, the experimental sites were first ploughed and then fully covered with a black polypropylene woven fabric that prevents growth of weeds and the emergence of arthropods from the soil. We subsequently placed 20 walk-in experimental cages (2 m × 2 m × 1.75 m, L×W×H), made of insect nets with a zippered opening on one side (1 mm mesh size; Mononet 1000, Rovero Systems B.V., the Netherlands (Bukovinszky et al., 2017)). Cages were laid out in two rows of ten on an area of 34 m × 10 m, with a distance of 4 m between the two rows and a distance of 1 m between cages within each row (Fig. S5.1).

After establishment of the cages, the bottom edges and corners of each cage were sealed with polyethylene film which was additionally secured with sand bags. Each cage thus represented a confined space which kept all experimental arthropods in and kept all other arthropods and vertebrates out. A drip irrigation system was installed in all cages to be able to sufficiently water the experimental wheat plants without having to access the cages.

We applied four evenness treatments and a control treatment in which no arthropod predators were present (Fig. S5.1). In all four evenness treatments, we introduced four species of arthropod predators amounting to 16 individuals in total. The evenness treatments varied from highly uneven to completely even and consisted of (E1) one, two, three and ten individuals of the four species, respectively; (E2) one, three, five and seven individuals of the four species, respectively; (E3) three individuals of two species each and five individuals of the other two species each, and (E4) four individuals of each of the four species. We randomly assigned each of the five treatments (four evenness treatments and one control treatment) to four cages (Fig. S5.1). To be able to examine the effects of species identity independently from the evenness treatment, we carried out the experiment for four rounds. In each round the total number of individuals, species and evenness treatments were the same but a different species was the most abundant, the second most abundant, the third most abundant and the least abundant species in all the treatments of that round (Table S5.1). The total sample size of our study was therefore 80.

At the start of the first round, the polypropylene woven fabric was removed from the soil of each cage to provide the arthropod predators with near-natural soil conditions. Prior to the introduction of the experimental plants and arthropods, the soil was cultivated again to eliminate any arthropods remaining under the fabric. Subsequently, six pitfall traps (white plastic beakers, dimensions: top diameter 98 mm, height 151 mm, filled with about 2/3 water) and four sticky traps (28 cm × 12 cm; Horiver®, Koppert B.V., Berkel en Rodenrijs, the Netherlands) were set within each cage. When no more arthropods were captured by these traps for three days in a row, we removed the traps and moved the first batch of wheat plants into the cages. Sixteen pots with five wheat plants each were placed into each cage (Fig. S5.2) with the top of the pots level with the soil surface so that ground-active arthropods could easily move between different wheat plants. Aphids were inoculated on the wheat plants of the central four pots (see below) when the growth stage of the plants was around the watery ripe stage (BBCH 70) as this provides the best conditions for aphid growth (Watt, 1979). After data collection was finished, we manually collected any observed arthropod predators and removed the aboveground biomass of the wheat plants. We then set six pitfall traps and four sticky traps within each cage to capture any remaining arthropod predators, the abundance of recollected arthropod predators was recorded, recollected living arthropod predators were set free and not used for the next round. Two days before we moved in the wheat plants of the next round, we removed the traps and cultivated the soil in each cage to eliminate weed seedlings and potentially remaining arthropod predators. This procedure was repeated between the first and second round, the second and third round and the third and fourth round. After the fourth round finished, six pitfall traps and four sticky traps were set for six days to recollect introduced arthropod predators. The duration of each experimental round was about one month (from wheat plants being moved in until soil was cultivated).

Preparation of the plants and arthropods

Four batches each of 320 pots (volume: 10 L, dimensions: top diameter 28 cm, base diameter 24 cm, height 22.5 cm) of organic wheat were sown in a greenhouse at the experimental farm of Wageningen University & Research. The first batch was sown on 8 March 2021 and each subsequent batch was sown about one month after the previous batch to keep the growth stage of the wheat consistent between the four experimental rounds. Soil composition was 91% peat, 7% loam and 2% vermiculite (mass ratio). Eight to ten seeds were sown in each pot and after germination the weakest plants were removed to have five healthy wheat plants per pot. After the removal of the superfluous wheat plants, all pots were covered with fine mesh to prevent arthropods from colonizing the pots. The potted wheat plants were checked frequently and any observed arthropod or weed that had managed to colonize the pots were removed manually. The fine mesh was removed when the wheat plants were moved into cages.

The aphids, lady beetles and mirid bugs were bought from Katz Biotech AG (Baruth/Mark, Germany). The carabid beetles and spiders were collected by deploying a total of 42 live pitfall traps (same as the pitfall traps in the cage but without trapping liquid) that were placed around Wageningen (Fig. S5.3). The pitfall traps were installed in field margins and checked every two to three days. The targeted arthropods were collected and all other arthropods were released. Before the targeted arthropods were introduced, collected carabid beetles and spiders were kept in plastic containers separately and stored in dry and cool chamber (moisture 50% to 60%, temperature 20 to 25 °C). Cloth soaked with water was placed in each tube container to keep it moist. The cloth was replaced two to three times per week.

Data collection

In each cage and each round, we introduced approximately 600 adult apterous *S. avenae* on the wheat plants of the central four pots (i.e., about 150 aphids per pot). Aphids were inoculated on the top three leaves of the plants using a fine hair brush (Luo et al., 2016). We then closed the cage and allowed the aphids to establish. After two days we recorded all observed live aphids on the wheat plants (the first aphid count). In each of the evenness treatments, the arthropod predators were introduced immediately after the first aphid count by randomly placing them in the outer twelve pots in each cage to avoid initial intraguild predation. After the aphids had been recorded and the arthropod predators had been introduced in all cages, they were left undisturbed until the second aphid count on the sixth day. We only counted the aphids that were on plants as the dropped live aphids can quickly return to plants canopy if they were not predated by ground-dwelling arthropod predators (Winder et al., 1994). Thus, abundance of the aphids on plants can also reflect predation by ground-dwelling arthropod predators. Aphid growth rate was calculated for each cage as the number of aphids of the second count divided by the number of aphids of the first count (Garratt et al., 2018). The data of four cages in the first round, two cages in the second round, four cages in the third round and one cage in the fourth round were excluded from the analyses as we found non-experimental natural enemies or recollected more experimental arthropod predators than had been introduced in these cages.

Statistical analysis

All analyses were conducted in R version 4.2.1 (R Core Team, 2022b). In a first step, we used a linear regression model to analyse whether aphid growth rate differed between the different treatment levels and whether this differed between rounds (and therefore the identity of the most dominant species). This model included treatment, round and the interaction between treatment and round as explanatory variables. Since the interaction between treatment and round was statistically significant (see Results section), we subsequently compared aphid growth rate between different treatments for each round separately, using linear models with treatment as explanatory variable. Pairwise comparisons were made with Tukey HSD tests using the glht function in the multcomp package (Hothorn et al., 2022).

The significant interaction between treatment and round (see Results) indicates that effects of evenness differed across rounds and/or the identity of the most dominant species in each round. To better disentangle these effects, we further analysed the effects of the evenness treatments while taking into account the effects of the abundance of the individual arthropod predator species. Because the experiment was carried out over a period of more than four months, we corrected for the inevitable inherent differences in aphid growth rate between the rounds by using the relative growth rate as a response variable. Relative aphid growth rate was determined as the growth rate in each cage with an evenness treatment divided by the mean growth rate of the control treatment in that round. A relative growth rate of 1 would then indicate that the aphid growth rate of the evenness treatment was the same as the growth rate without arthropod predators, and relative growth rates below 1 would indicate suppression of aphid growth. We used linear mixed effects models (package glmmTMB with gaussian distribution (Magnusson et al., 2022)) and an information theoretic approach to analyse the effects of the different evenness treatments and the abundance of different species of arthropod predators on the relative growth rate. We first constructed a global model that included the evenness treatment and the number of individuals of each of the four species as fixed effects and round as random effect. We then constructed an all-subsets model set consisting of all possible combinations of the fixed variables. Given the sample size, we restricted the model set to all possible combinations with a maximum of three fixed effect variables to limit model complexity and the total number of models in the model set (Burnham et al., 2011). Using package MuMIn (Bartoń, 2022), we ranked the models in the model set (Table S5.2) based on their Akaike Information Criterion values corrected for small sample size (AICc) and calculated full-model averaged parameter estimates and parameter weights based on all models with Δ AICc < 6 (Burnham et al., 2011). Furthermore, because our results suggested a linear response pattern between relative aphid growth rate and the evenness treatment, we analyzed the shape of the relationship between arthropod predator evenness and aphid growth rate. To this end, we calculated Pielou’s index (using vegan package (Oksanen et al., 2022)) for each treatment to express the different evenness treatments as a continuous variable, and re-ran the highest ranked model of the previous analysis with the continuous Pielou’s index variable instead of the categorical evenness treatment variable. In this model, the arthropod predator abundance variable and Pielou’s index variable were standardized (mean-cantered and divided by 1 SD) to aid comparison of effect sizes.

Results

Our analysis of aphid growth rate per round showed that growth rate was significantly affected by treatment ($F_{4, 49} = 222.5$, $P < 0.001$), round ($F_{3, 49} = 7.572$, $P < 0.001$) and their interaction ($F_{12, 49} = 22.34$, $P < 0.001$). Overall, mean aphid growth rate was 67% lower in the treatments with arthropod predators than in the control treatment without arthropod predators. The presence of arthropod predators significantly reduced aphid growth rate in all four rounds, but the magnitude of the effect differed between round and evenness treatment (Fig. 5.1). We did not find significant differences in aphid growth rate between the four evenness treatments in the first round in which the mirid bug was the most dominant species. However, in the third and fourth round, with two ground-dwelling guilds (spider and carabid beetle respectively) as the most dominant species, aphid growth rate was generally lowest in the most even treatment (E4) and differed significantly from aphid growth rates in the most uneven treatment (E1). In contrast, in the second round, with lady beetle as the most dominant species, aphid growth rate was lowest in the most uneven treatment (E1), although the difference was only significant compared to treatment E3 (Fig. 5.1).

The combined analysis of the effects of evenness and the effects of the abundance of different species showed that relative aphid growth rate was mainly affected by the abundance of lady beetles and the evenness treatments. These two variables featured in all models in the best subset, while the abundance

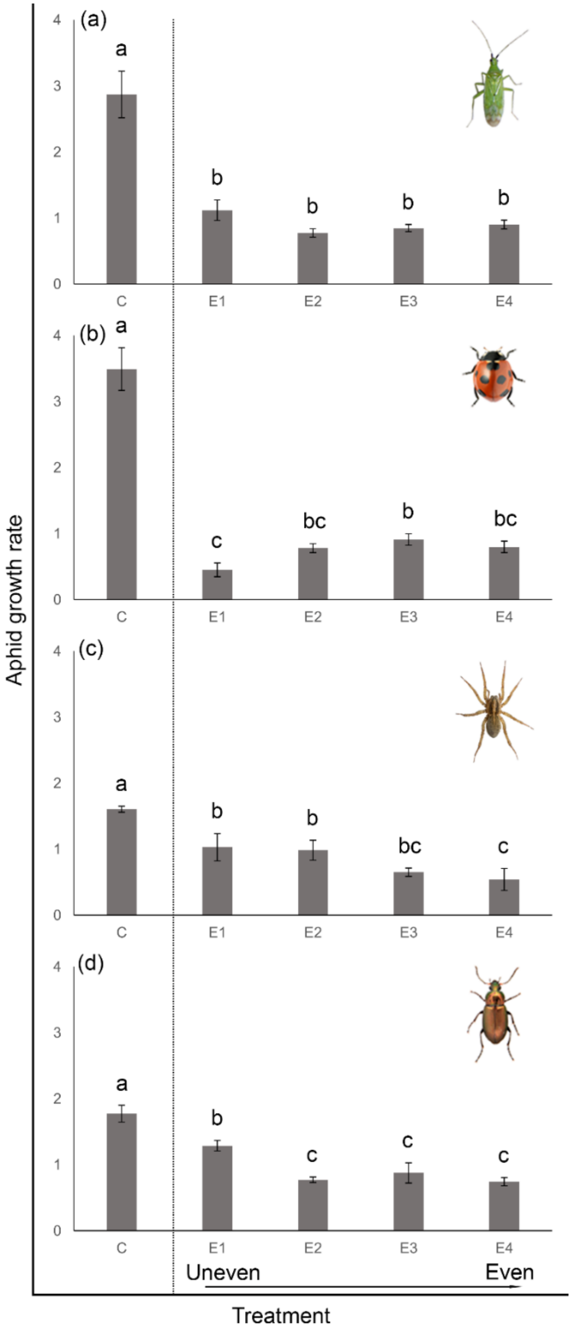


Fig. 5.1. Effects of different treatments (C: control treatment with no natural enemies; E1 to E4: evenness treatment with natural enemies) on mean ± SE of aphid growth rate in separate round: (a) 1st round, with *Macrolophus pygmaeus* as the most dominant species, (b) 2nd round, with *Coccinella septempunctata* as the most dominant species, (c) 3rd round, with *Trochosa ruricola* as the most dominant species and (d) 4th round, with *Poecilus cupreus* as the most dominant species (detailed community composition presented in Table S5.1). Different letters indicate significant differences among treatments (adjusted P value < 0.05).

Table 5.1. Model selection and model averaging results for effects of abundance of four natural enemies and different evenness treatment on relative growth rate of aphids. Candidate models (Δ AICc < 6) are ranked in order of increasing differences in corrected Akaike Information Criterion. Model averaged parameter estimates (β), 95% confidence intervals (CI) and relative importance (ω_p) are given for each explanatory variable. Confidence intervals not overlapping zero are indicated in bold. The number of parameters (k) and Akaike model weight (ω_m, which indicates the probability that a model is the best approximating model in the candidate set) are shown for each model.

Model No.	Explanatory variables							k	AICc	Δ AICc	ω_m
	Carabid beetle	Lady beetle	Mirid bug	Spider	E2	E3	E4				
1		-0.056	-0.018		-0.091	-0.109	-0.151	8	-113.1	0	0.632
2	0.013	-0.047			-0.090	-0.109	-0.152	8	-110.4	2.76	0.159
3		-0.052			-0.093	-0.114	-0.156	7	-110.3	2.78	0.157
4		-0.049		0.006	-0.093	-0.114	-0.156	8	-108.1	4.98	0.052
β	0.002	**-0.054**	-0.012	0.000	**-0.091**	**-0.110**	**-0.152**				
Lower 95% CI	-0.009	**-0.070**	-0.032	-0.004	**-0.147**	**-0.169**	**-0.209**				
Upper 95% CI	0.013	**-0.037**	0.009	0.005	**-0.035**	**-0.051**	**-0.096**				
ω_p	0.16	**1**	0.63	0.05	**1**	**1**	**1**				

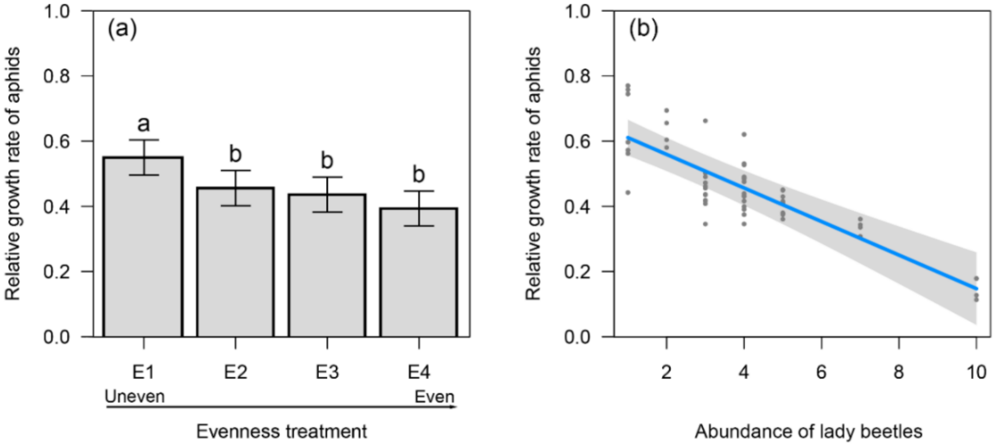


Fig. 5.2. Effects of different evenness treatments (a) and abundance of lady beetles (b) on relative aphid growth rate. For figure (a) model-estimated means are shown with error bars indicating SE, and for figure (b) fitted line indicates the estimate effects and shaded area indicates 95% confidence interval.

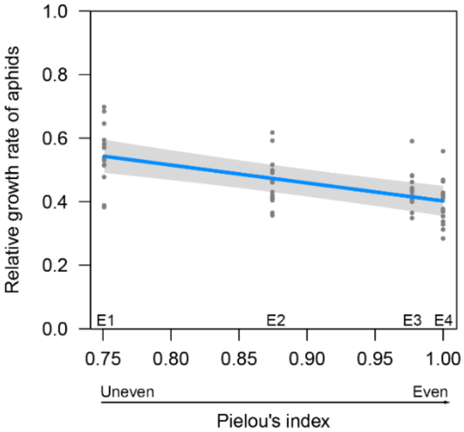


Fig. 5.3. Linear relationship between Pielou's index of each evenness treatment (instead of the categorical evenness treatment variable (E1, E2, E3 and E4) in Fig. 5.2a) and relative aphid growth rate. Fitted line indicates the estimate effects and shaded area indicates 95% confidence interval.

of the other three species each featured in only a single model (Table 5.1). Relative aphid growth rate was negatively related to the abundance of lady beetles (Table 5.1; Fig. 5.2b) and differed among evenness treatments (Table 5.1; Fig. 5.2a), with the most even treatment (E4) resulting in the largest reduction in relative aphid growth rate and the most uneven treatment (E1) resulting in the smallest reduction. Replacing the categorical evenness treatment levels with the standardized continuous Pielou's index showed that the relative aphid growth rate declined linearly with increasing evenness of arthropod predator communities (Fig. 5.3). However, the effect of evenness was less pronounced than that of abundance of lady beetles (standardized parameter estimates of respectively -0.055 and -0.114).

Discussion

Compared to community species richness and abundance, the contribution of evenness to ecosystem functioning is relatively poorly studied (Hillebrand et al., 2008; Wittebolle et al., 2009; Snyder, 2019). Here we controlled for the total species richness and abundance of natural enemy communities and showed that the effect of evenness of experimental natural enemy communities on natural pest control depends on the identity of the most dominant species in the community. However, after accounting for the abundance of the different predator species, we found positive evenness effects on pest suppression that are additional to the effects of species identity. Our results furthermore suggest a linear relationship between natural enemy evenness and pest growth reductions.

In line with previous studies that produced inconsistent results (Crowder et al., 2010; Rusch et al., 2015; Mace & Mill, 2017; Riggi et al., 2017; Dainese et al., 2019; Yuan et al., 2019), we also found that effects of evenness on natural pest control were mixed (Fig. 5.1). One of the few studies that found a clear positive effect of evenness on pest control was done by Crowder et al. (2010) who used a strictly experimental approach that accounted for effects of natural enemy abundance, species richness and identity. Likewise, in our experimental study we found positive effects of evenness on pest control when accounting for the abundance of the most effective predator species. In contrast, many field studies showed that effects of natural enemy evenness on pest control were neutral or even negative (Rusch et al., 2015; Riggi et al., 2017; Dainese et al., 2019). One possible explanation for the discrepancy between the results of cage experiments and field studies could be the inevitable incomplete sampling in field studies (Engel et al., 2017; Hambäck et al., 2021). This means that the true evenness may not be properly assessed in field studies, possibly causing bias in the relationship between natural enemy evenness and pest suppression efficiency. Furthermore, in real ecosystems it is often difficult to disentangle the separate effects of natural enemy evenness from other community metrics such as species richness and abundance. For example, environmental conditions that support higher natural enemy evenness can simultaneously promote their abundance, which results in a correlation between natural enemy evenness and abundance (Aldebron et al., 2020; Blubaugh et al., 2021) that makes it impossible to disentangle their effects. The inconsistent results between experimental and field studies, and the stronger effects of species identity than evenness in the present study, indeed suggest that effects of evenness in real ecosystems are often obscured by effects of abundance, species richness and/or species identity and only become apparent when these factors are accounted for. Furthermore, the natural enemy communities in experimental studies are often composed of functionally and taxonomically distinct species. In our study, the four species of arthropod predators were from four different families and differed greatly in e.g., morphology, behaviour and diel activity (Bayram, 1995; Lövei & Sunderland, 1996; Elliott et al., 2000; Nissinen et al., 2017). In real ecosystems, natural enemy communities are generally composed of many species that are more closely taxonomically related and/or functionally redundant, which may result in larger ecological niche overlap and more intense inter-specific competition (Michalko & Pekar, 2015; Wong, 2019). Although the natural enemy communities in our experiment comprised of functionally and taxonomically contrasting species, the evenness of the communities resembled values found in real-world agroecosystems. In a field study of natural enemy communities in winter wheat fields across four European countries, approximately 80% of the fields had pooled spider and carabid beetle communities with Pielou's index that were within the range of this study (Met et al., 2023).

Species identity, expressed as the abundance of the different individual species, had a more pronounced effect on aphid suppression than evenness. The abundance of the two flying natural enemies was negatively related to relative aphid growth rate (Table 5.1), particularly for *Coccinella septempunctata*

(Fig. 5.2b) and to a lesser extent for *Macrolophus pygmaeus* (Fig. S5.4a). In the experimental round where *C. septempunctata* was the most dominant arthropod predator, the highest suppression of aphid growth rate was observed in the most uneven treatment that comprised the largest number of individuals of lady beetles (Fig. 5.1b). The abundance of the two ground-dwelling natural enemies, *Poecilus cupreus* and *Trochosa ruricola*, was not notably related to the aphid growth rate (Table 5.1, Fig. S5.4b, c) and when these species dominated the arthropod predator communities, aphid growth rate suppression was generally higher in the most even treatment (Fig. 5.1c, d). This is generally in line with previous studies that found flying natural enemies to be more effective than ground-dwelling ones in suppressing aphid pests (Schmidt et al., 2004; Holland et al., 2008; Thies et al., 2011). *C. septempunctata* has been flagged before as a particularly effective, specialist predator of aphids (Straub & Snyder, 2006; Caballero-López et al., 2012). Each *C. septempunctata* individual can kill more than 50% of the *Acyrthosiphon pisum* individuals they encounter and dislodge the majority of the rest of the aphids from crop plants (Minoretti & Weisser, 2000). A similar predation efficiency was observed in the present study, with only 45% of the inoculated *S. avenae* remaining on the wheat plants in the most uneven treatment where *C. septempunctata* was the most dominant arthropod predator (Fig. 5.1b). One reason for the different suppression efficiency between flying and ground-dwelling natural enemies could be the location of aphids on wheat plants. *S. avenae* generally infests wheat ears and prefers to stay in the upper parts of plants. Even though *P. cupreus* and *T. ruricola* were reported to be able to climb on plant to prey aphids (von Berg et al., 2012; Chiverton, 1988), we did not observe this behaviour in our experiment. The aphids are generally more accessible to flying natural enemies than to ground-dwelling ones (Holland et al., 2008). However, aphids may drop down from plants to avoid or escape from flying natural enemies (Minoretti & Weisser, 2000; Zhang et al., 2019) and ground-dwelling natural enemies can complement flying ones by preying on the dropped aphids and preventing aphids to spread to other plants (Losey & Denno, 1998).

Another reason for the predominant role of lady beetles in suppressing aphids could be because it may have been less affected by intraguild interference. Even though our experiment did not enable us to directly identify intraguild interactions, such interactions can be inferred from the recollection rates of the natural enemies at the end of each survey round. The recollection rate was highest for lady beetles, with an average recollection rate of 99%, followed by carabid beetles (85%), mirid bugs (56%) and spiders (44%). Lady beetles are specialist aphid predators but sometimes also prey on mirid bugs as alternative food source when aphid densities are insufficient (Lucas & Alomar, 2000; Trotta et al., 2015). In contrast, mirid bugs can only prey on small arthropods and thus are at a disadvantage in the presence of lady beetles. The two ground-dwelling predators are generalist predators that also consume large arthropods. In agro-ecosystem, carabid beetles are known to predate on spiders, while there is little evidence that spiders predate on carabid beetles (Lang, 2003; Davey et al., 2013; Roubinet et al., 2018). We cannot assert that non-recollected mirid bugs and spiders were predated in our study, but the low recollection rate of mirid bugs and spiders could imply they were negatively affected by intraguild interactions which may have decreased their aphid suppression effectiveness.

Conclusion

Maximizing pest regulation services by natural enemies requires a thorough understanding of how natural enemy diversity and community composition affect pest suppression. While many previous studies found positive effects of natural enemy abundance and species richness on natural pest control (Jonsson et al., 2017; Greenop et al., 2018; Dainese et al., 2019), our study found that evenness and the identity of the dominant species play vital roles in suppressing aphid pests. In our experimental system, the most efficient predator, *Coccinella septempunctata*, mainly determined the effectiveness of aphid control by the natural enemy communities. This provides support for the hypothesis that ecosystem service provision is generally the product of abundance and efficiency of the dominant species (Winfree et al., 2015; Hillebrand et al., 2008), resulting in maximum natural pest control when the most efficient species dominates the community. When a less efficient aphid predator dominated our natural enemy communities, pest control services were significantly lowered, which provides an additional explanation for why managing for more natural enemies through provision of semi-natural habitat does not always result in enhanced pest control (Holland et al., 2016; Tscharntke et al., 2016; Karp et al., 2018). If management increases the dominance of a less-efficient predator or enhances intra-guild predation of species that are highly efficient natural enemies, pest control may even be reduced. However, on top of the effect of species identity, our study finds more subtle positive effects of community evenness on aphid suppression. Because of the linear nature of the relationship, increasing evenness will result in straight-forward increases in pest control with possible associated benefits to community resilience and stability (Wittebolle et al., 2009; Wan et al., 2014). Evenness is therefore an important component contributing to the functioning of natural enemy communities and the services they provide. However, evenness effects on pest control may be difficult to demonstrate in real-world ecosystems, because here evenness is generally correlated with species-richness and abundance.

Acknowledgements

We are grateful for the experiment assistance of Jan van Walsem, Rohan van Genderen, John van der Lippe and Rinie Verwoert.

Supplementary materials

Table S5.1. Abundance of four species of natural enemies that was introduced in each cage for each round and treatment.

Species	Round 1				Round 2				Round 3				Round 4			
	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4	E1	E2	E3	E4
Macrolophus pygmaeus	10	7	5	4	3	5	5	4	2	3	3	4	1	1	3	4
Coccinella septempunctata	3	5	5	4	10	7	5	4	1	1	3	4	2	3	3	4
Trochosa ruricola	1	1	3	4	2	3	3	4	10	7	5	4	3	5	5	4
poecilus cupreus	2	3	3	4	1	1	3	4	3	5	5	4	10	7	5	4

Table S5.2. Candidate model set explaining how abundance of four different natural enemies and different evenness treatments affect relative growth rate of aphids. Models are ranked in order of increasing differences in corrected Akaike Information Criterion (ΔAICc). Akaike model weights (ω) indicate the probability that a model is the best approximating model in the candidate set. k indicates the number of parameters in the model.

Model No.	Explanatory variables							k	AICc	Δ AICc	ω_m
	Carabid beetle	Lady beetle	Mirid bug	Spider	E2	E3	E4				
1		-0.056	-0.018		-0.091	-0.109	-0.151	8	-113.1	0	0.631
2	0.013	-0.047			-0.090	-0.109	-0.152	8	-110.4	2.76	0.159
3		-0.052			-0.093	-0.114	-0.156	7	-110.3	2.78	0.157
4		-0.049		0.006	-0.093	-0.114	-0.156	8	-108.1	4.98	0.052
5		-0.058	-0.023					5	-97.3	15.86	<0.001
6	0.038			0.033	-0.082	-0.100	-0.141	8	-96.9	16.25	<0.001
7	0.063		0.035	0.051				6	-96.5	16.65	<0.001
8	0.012	-0.051	-0.020					6	-96.5	16.65	<0.001
9	0.028	-0.035		0.016				6	-96.5	16.65	<0.001
10		-0.063	-0.028	-0.012				6	-96.5	16.65	<0.001
11	0.024	-0.050						5	-94.8	18.28	<0.001
12		-0.052						4	-92.4	20.76	<0.001
13		-0.049		0.006				5	-90.4	22.76	<0.001
14	0.042			0.033				5	-87.3	25.85	<0.001
15	0.034				-0.077	-0.095	-0.140	7	-83.4	29.68	<0.001
16	0.037		0.008		-0.078	-0.096	-0.142	8	-81.4	31.76	<0.001
17				0.029	-0.088	-0.110	-0.150	7	-78.7	34.44	<0.001
18	0.037							4	-76.7	36.42	<0.001
19			0.003	0.030	-0.089	-0.112	-0.151	8	-76.1	38.67	<0.001
20	0.039		0.004					5	-74.4	38.67	<0.001
21					-0.083	-0.104	-0.148	6	-71.6	41.50	<0.001
22				0.029				4	-70.5	42.64	<0.001
23			-0.010		-0.081	-0.102	-0.144	7	-70.1	43.03	<0.001
24			-0.003	0.028				5	-68.1	44.99	<0.001
25								3	-65.4	47.69	<0.001
26			-0.015					4	-64.8	48.31	<0.001

Fig. S5.1. Google Earth satellite image (taken on 30/May/2021) of experimental site (51°59'47" N, 5°39'36" E, Wageningen, the Netherlands) indicates cage distribution and allocation to different treatments. Circles with different colors represent different treatments.

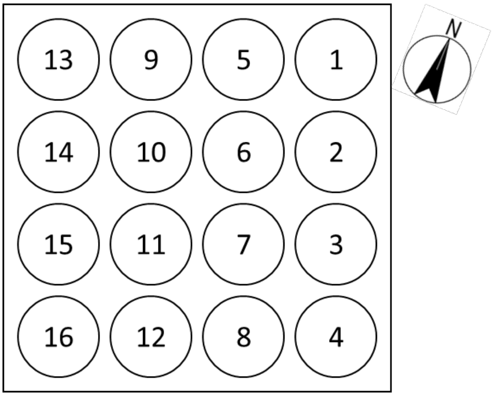


Fig. S5.2. Pot allocation of each cage. Pots were always numbered starting from the most north-eastern pot and then from north to south in each cage. Aphids were only inoculated on the wheat plants of central four pots (numbered as 6, 7, 10 and 11) for all cages.

Fig. S5.3. The approximate position of pitfall traps installed to collect *Poecilus cupreus* and *Trochosa ruricola*. Latitudes and longitudes indicate the geographic position of the four corners of each satellite image. Pitfall traps installation can be split into 3 rounds and the time of each round is presented. All pitfall traps were removed in the beginning of October after experiment finished. The satellite images are from Google Earth and were taken on 30/May/2021.

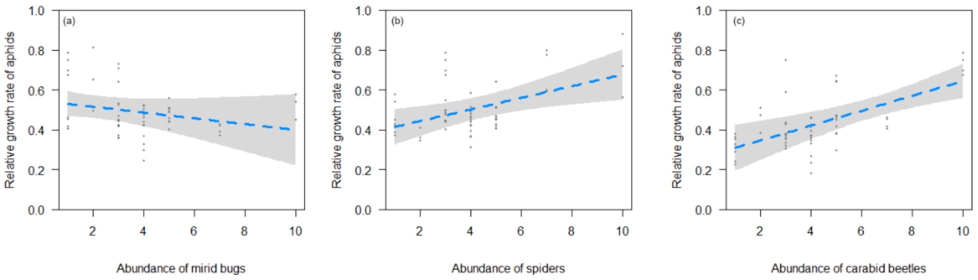
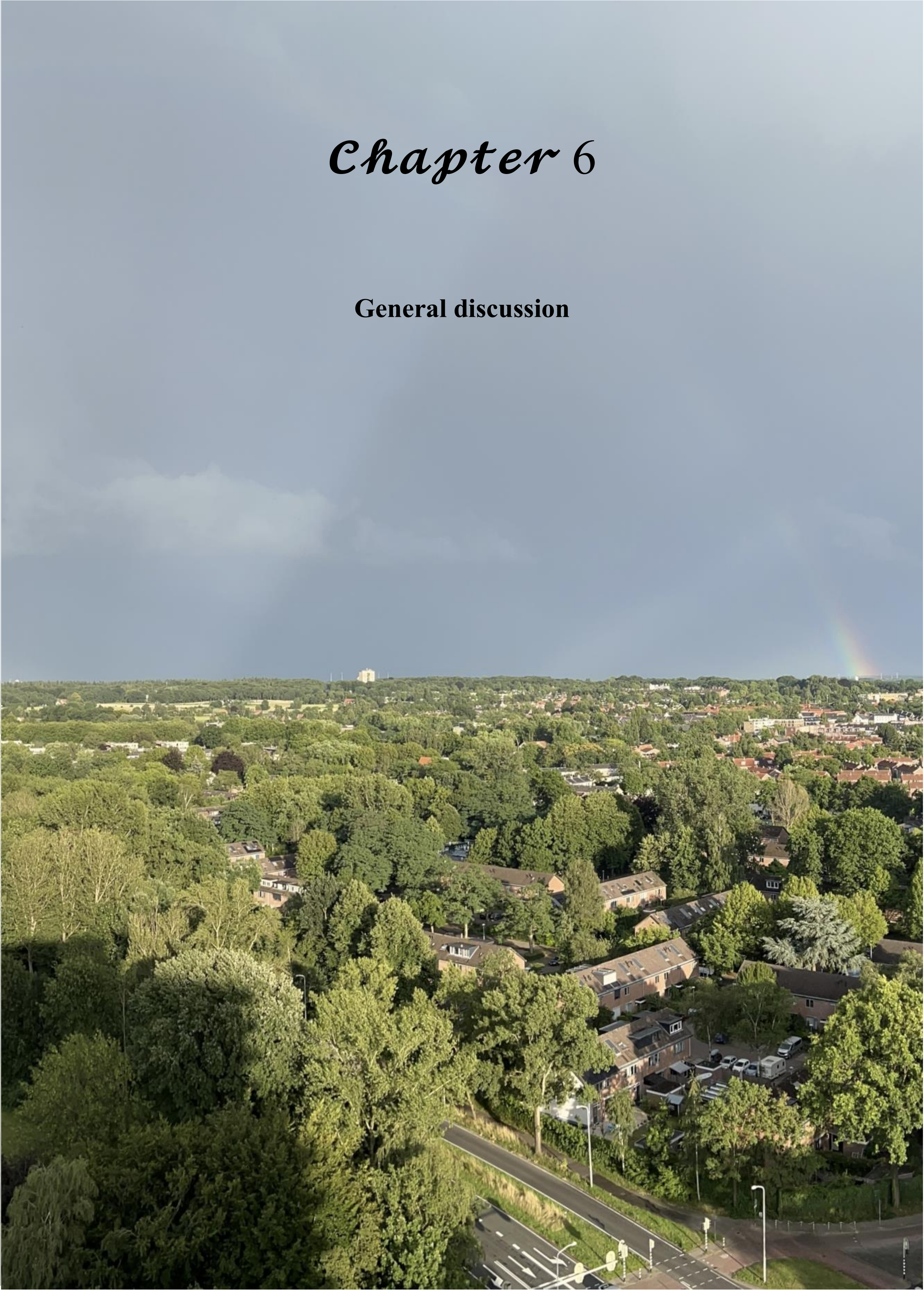


Fig. S5.4. Effects of abundance of (a) mirid bugs, (b) spiders and (c) carabid beetles on relative aphid growth rate. Dashed lines indicate the estimate effects and shaded areas indicate 95% confidence intervals.

Chapter 6

General discussion



Introduction

The work presented in this thesis aimed to enhance the evidence base of the concept of ecological intensification from the perspective of an important regulating service – natural pest control. As an alternative paradigm for current intensive agricultural production, ecological intensification proposes to better exploit the ecosystem services occurring naturally on farmland by enhancing the species that can provide these services. Thus, a win-win situation can be achieved where agrobiodiversity can be enhanced and agricultural productivity can be maintained simultaneously (Bommarco et al., 2013). The number of studies that provide proof of concept of ecological intensification is increasing continuously, but there are still considerable knowledge gaps that hinder the agricultural sector to implement ecological intensification more widely. One knowledge gap is that studies examining the effects of ecological intensification on natural enemies often focus on the response of a single species guild to a single environmental factor or management practice. Since natural enemies come from a wide range of different arthropod orders and families, different natural enemy guilds may respond inconsistently to the same environmental factor or practice (Rand et al., 2012; Zhao et al., 2013; Karp et al., 2018; Li et al., 2018). Furthermore, multiple environmental factors or management practices may interact with each other (Ricci et al., 2019; Aguilera et al., 2020; Krimmer et al., 2022) and these interactions can mask the net effects of a single practice in conserving agrobiodiversity or ecosystem service delivery. This may result in the effectiveness of a practice to vary with the local conditions in which it is being implemented (Kleijn et al., 2006; Karp et al., 2018; Martin et al., 2019). Another knowledge gap is that, compared to how natural pest control service delivery is affected by natural enemy abundance and species richness, we know relatively little about the relationship between pest control service delivery and natural enemy evenness and community composition (Snyder, 2019). A better understanding of the underlying mechanisms that explain how natural enemy community characteristics affect natural pest control effectiveness can help us formulate clearer suggestions that how to make agricultural production more sustainable. This thesis examined how multiple guilds of natural enemies responded to multiple environmental factors at different spatial scales or field management practices and how pest control effectiveness was affected by natural enemy community with different evenness and composition but the same abundance and species richness. Therefore, this thesis provides more evidence-based studies that can deepen our understanding of the response patterns of natural enemies to surrounding environmental factors and can further help us to better implement ecological intensification in real agroecosystems.

In this thesis, I first examined how wildflower strips, a practice that is widely advocated by academic sector but not highly valued by farmers, affect the abundance of natural enemies, natural pest control service and crop yield. I examined how floral resources moderated the effects of wildflower strips and how the effects of the floral resources on natural enemy abundance, natural pest control service and crop yield were affected by on-field management (Chapter 2). In Chapter 3, I carried out a meta-analysis across four countries in north-western Europe to examine how activity density, species richness and evenness (α-diversity) of carabid beetle and spider communities were affected by landscape complexity, land-use intensity and local soil characteristic. I distinguished between the response of dominant and non-dominant species to test if enhancing ecosystem services and conserving agrobiodiversity are compatible objectives. In chapter 4, using the same data of Chapter 3, I examined how β-diversity of carabid beetles and spiders was affected by distance, landscape complexity, land-use intensity and local soil characteristic in pairs of fields to understand the mechanisms of how natural enemy species turn-over. In Chapter 5, I carried out a strictly controlled experiment, in which *S. avenae* aphid colonies were exposed in experimental cages to natural enemy communities that had the same abundance and species richness but that differed in evenness and dominant species to understand the underlying mechanisms of how natural enemy evenness and composition affected natural pest control effectiveness.

Different guilds of natural enemies respond inconsistently to agricultural intensification

The core aim of agricultural intensification is to pursue higher agricultural productivity per unit area and this process has been demonstrated to be the main driver of agrobiodiversity loss (Flynn et al., 2009; Kleijn et al., 2009; Ekroos et al., 2020). However, results of this thesis found that the relationship between different guilds of natural enemies and agricultural intensification may be more complex.

One factor that is driving the agricultural intensification is the utilization of agrochemicals like synthetic fertilizers or pesticides (Herzog et al., 2006). In Chapter 2, I tested how the abundance of three guilds of ground-dwelling natural enemies was affected by the application of fertilizer or insecticide. The results suggest that different guilds displayed inconsistent response patterns to the application of fertilizer. The abundance of both carabid beetles and spiders was negatively related with the application of fertilizer while the abundance of staphylinid beetles was positively related with it. The inconsistent responses of different guilds ultimately neutralized the effects of applying fertilizers on the abundance of all ground-dwelling natural enemies combined and could be an important reason why applying fertilizer did not affect the pest control effectiveness. For insecticide, I observed pronounced negative effects on spiders, but not on carabid beetles and staphylinid beetles. Even though spraying insecticides played a vital role in suppressing aphids, it can simultaneously reduce natural enemies (Bommarco et al., 2011; Regan et al., 2017). Therefore, from a long-term perspective, the indirect negative effects of insecticides on natural pest control may outweigh its direct positive effects on suppressing aphids and ultimately cause the resurgence of target pests or outbreaks of secondary pests (Hill et al., 2017; Janssen and van Rijn, 2021).

One of the consequences of agricultural intensification is a significant increase in land-use intensity (van der Sluis et al., 2016). Since crop yield represents the end result of all short- and long-term management practices, I used crop yield as a proxy for land-use intensity in Chapter 3 and 4. In Chapter 3, I found strong support that species richness of carabid beetles was positively related with land-use intensity, however, activity density, species richness and evenness of spiders all displayed a potentially negative trend with land-use intensity. This suggests inconsistent responses by carabid beetles and spiders to land-use intensity. In line with some previous studies, I also found that spiders are more sensitive to land-use change and more susceptible when land-use intensity is high (Hendrickx et al., 2007; Batáry et al., 2008; Lessard-Therrien et al., 2018). This could partly be explained by the fact that spiders are generally at a lower trophic level than carabid beetles as carabid beetle can prey on spiders but spiders can hardly prey on carabid beetles (Lang, 2003; Davey et al., 2013).

In Chapter 4, I unexpectedly did not find any strong support for relationships between β-diversity of both carabid beetles and spiders and land-use intensity. However, I found that community similarity of carabid beetles showed a negative (non-significant) trend with land-use intensity difference while spiders showed a positive trend. This finding suggests that even though the effects of land-use intensity on β-diversity were less pronounced than those on α-diversity, carabid beetle and spider communities also displayed inconsistent response patterns. One reason for the less pronounced effects on β-diversity could be that I sampled arthropods only in intensively managed wheat fields, which resulted in the conditions of different sampling site being quite similar. Furthermore, communities of both carabid beetles and spiders were dominated by widespread species that can be found across the entire continent. These widespread species generally are well-adapted to the disturbance in arable fields and are robust to intensive management practices (Clough et al., 2005; Öberg and Ekbom, 2006; Öberg et al., 2007). This could indicate that these dominant species keep arthropod communities relatively stable across a range of land-use intensity.

Quality and quantity of semi-natural habitats play vital roles in conserving natural enemy diversity

The majority of the arthropod natural enemies in agricultural landscape are highly mobile and rely on resources from non-crop patches for most of the year. Semi-natural habitats in agricultural landscapes are therefore important for conserving agrobiodiversity. Semi-natural habitats include field margins, ditch banks and roadside verges and are important shelters for arthropod natural enemies as they can provide less-disturbed overwintering sites and other resources that are unavailable on arable fields (Holland et al., 2016). In highly simplified agricultural landscapes, creating new semi-natural habitats is predicted to be an effective way to promote the abundance and diversity of natural enemies, which can then enhance natural pest control services (Wäckers & van Rijn, 2012; Veres et al., 2013; Alignier et al., 2014).

In Chapter 2, I found that improving available resources in semi-natural habitats could be a cost-effective alternative for creating new semi-natural habitats. I found that the floral resources in field margins can promote the abundance of arthropod natural enemies. Furthermore, I found that it was the actual floral resources that determined the effectiveness of attracting arthropod natural enemies regardless of whether they were provided by wildflower strips or by pre-existing field margins, which indicates that wildlife-friendly management of field margins to improve their quality can be as effective as establishing new wildflower strips. This can reduce the costs of enhancing natural enemies on arable land. Both carabid beetles and spiders benefited from higher floral resources. However, such positive effects did not extend far into the fields, higher abundance of spiders was observed up to 5 m into the fields and higher abundance of carabid beetles was only observed within the field margins. The positive effects of higher floral availability on crop yield also extended into fields for about 5 m only.

In Chapter 3, I found a strongly negative relationship between the proportion of cropland and evenness of carabid beetles and between the proportion of cropland and species richness of all spiders and non-dominant spider species richness and activity density. The negative relationship between landscape simplification and evenness of carabid beetles probably resulted from the somewhat different responses of the dominant and non-dominant carabid beetles. The activity density of dominant carabid beetle species displayed a positive trend with landscape simplification while activity density and species richness of non-dominant carabid beetle species displayed a negative trend with landscape simplification. Even though the response trends of dominant and non-dominant spiders on landscape simplification were the same, the negative effects of landscape simplification on non-dominant spiders were more pronounced. The stronger relationship between landscape simplification and spiders may even have caused the change in spider community composition, but not that of carabid beetles, across distance in Chapter 4. These findings highlight the importance of semi-natural habitats especially for non-dominant species which generally include the species of conservation concern (Pywell et al., 2012).

The vegetation structure of plant communities in semi-natural habitats is generally more complex than that of arable fields, and can therefore provide more niches for arthropod natural enemies (Söderström et al., 2001; Bartual et al., 2019). In particular, web building spiders can benefit from the complex vertical structure as different species can occupy different layers (Diehl et al., 2013). Furthermore, even though the majority of the carabid beetles and spiders cannot directly use the alternative food resources provided by semi-natural habitats, like pollen or nectar, these resources can attract flower-visiting insects which can be additional prey for arthropod natural enemies (Heiling et al., 2003; Wäckers, 2005). The results indicated a more pronounced effect of semi-natural habitats on non-dominant species than on dominant species for both carabid beetles and spiders. This could be because, compared to dominant species, non-dominant species are generally more vulnerable and rely more strongly on the less-disturbed semi-natural habitats. In Chapter 3, I found that a higher proportion of semi-natural habitats can promote the evenness of carabid beetles, which could indicate that one of the mechanisms why semi-natural habitats often enhance natural pest control services, as the positive effects on natural enemy evenness has been found to support a higher pest predation efficiency in experimental studies (Crowder et al., 2010; Chapter 5).

Interactive effects between environmental factors at different spatial scales on natural enemies are weak

Different practices can interact with each other, which may result in the final effects on promoting biodiversity or enhancing ecosystem services to be antagonistic, additive or synergistic. For example, Gao et al. (2008) found that natural enemy diversity and pest suppression effectiveness were not affected by the independent effect of intercropping or insecticide application, but were significantly affected by their interactive effects. Different environmental factors or management practices can interact with each other even they are implemented at different spatial scales. For example, Tamburini et al. (2016) found that the higher proportion of semi-natural habitats only promoted parasitism and predation rate of aphids in fields managed with conservation tillage. Further, they also found conservation tillage improved local habitat quality and compensated the negative effects of a low-quality landscape. However, in contrast to these studies, the results of this thesis suggested weak interactions between different environmental factors and management practices.

In Chapter 2, I examined whether the effectiveness of establishing wildflower strips was affected by whether I applied fertilizer or insecticide. However, I did not find any meaningful interactive effects between presence of wildflower strips or flower cover or species richness on one hand and the presence or absence of fertilizer or insecticide on natural enemies, aphids and wheat yields. This indicates that the effects of floral availability in field margins, fertilizers and insecticides operated independently and the joint effects were additive. In Chapter 3, I found that some models with interactions between land-use intensity, landscape composition and SOC content as explanatory variables were retained in a number of the candidate sets of best models that explaining the α-diversity of carabid beetles or spiders. However, the relative importance of all these interactive variables were less than 0.7 and all of their confidence intervals overlapped zero, which suggested the support for these interactions was generally very low. In Chapter 4, I surprisingly did not find any meaningful interactions between any of the land-use intensity, landscape composition or SOC content variables on one hand and geographic distance on the other in explaining β-diversity of carabid beetles and spiders.

There are other studies that examined the effects of multiple environmental factors or practices on natural enemy diversity and that found no or only weak interactive effects (e.g., Woltz et al., 2012; Rusch et al., 2013a; Redlich et al., 2021). However, the majority of the studies did find that interactions among environmental factors at different spatial scales play important roles in affecting diversity of natural enemies and shaping the effectiveness of natural pest control (e.g., Otieno et al., 2011; Martin et al., 2016; Tamburini et al., 2016; Ricci et al., 2019; Aguilera et al., 2020; Krimmer et al., 2022). These interactive effects can partly explain why the response patterns of natural enemies or natural pest control effectiveness were inconsistent when only aiming at a single environmental factor as the effects of a single environmental factor could be masked by other factors (Tscharntke et al., 2016; Karp et al., 2018). Therefore, even though the support of interactive effects in this thesis were generally low, it is still important to consider the effects of multiple factors and their interactions on natural enemies and associated natural pest control services.

Delivery of natural pest control services is an insufficient argument for natural enemy conservation

Ecosystem service provisioning has long been an important argument for agrobiodiversity conservation, as agricultural production relies heavily on the ecosystem services provided by the guilds occurring naturally on farmland (Millennium Ecosystem Assessment, 2005). However, recent studies have argued that ecosystem services are provided by a small subset of species (Kleijn et al., 2015; Winfree et al., 2015), and these species can generally easily be enhanced (Kleijn et al., 2015).

This thesis found similar results. In Chapter 3, I found a quite uneven distribution between dominant and non-dominant species, only 14% of carabid beetle species and 17% of spider species were classified as dominant species in at least one country, however, the relative abundance of these species were 90 % and 91 % respectively. In Chapter 4, using the same data, I further confirmed that the majority of the individuals of both carabid beetle and spider communities consisted of widespread species and the relative abundance of the species that occurred in all four countries accounted for 55% and 75% of carabid beetles and spiders respectively. Since the majority of the dominant or widespread carabid species were carnivores and the spiders species were active hunters, this indicates that these dominant or widespread species can provide substantial of natural pest control services. In this thesis, I found that these species were robust to agricultural intensification or landscape simplification.

In Chapter 5, I found that it was the abundance of the most efficient service provider that determined the effectiveness of a natural enemy community on aphid control. This finding supported the hypothesis that ecosystem service provision is generally the product of abundance and efficiency of the dominant species (Hillebrand et al., 2008; Winfree et al., 2015).

These findings highlight that maintaining the provision of ecosystem services and conserving agrobiodiversity are not the same objective as the majority of the ecosystem services are generally provided by a small subset of dominant species and these species have adapted to the agricultural disturbance regimes and can persist in agricultural landscapes (Kleijn et al., 2015). However, maintaining ecosystem service provisioning and conserving agrobiodiversity are not mutual exclusive, as the response patterns between dominant and non-dominant species were mostly similar (Chapter 3). Therefore, ecological intensification practices that aim at promoting ecosystem services providers can also benefit the non-dominant species that are of conservation concern.

Promoting natural pest control services via enhancing soil organic matter content may have potential

A vast body of research has examined how natural pest control effectiveness is affected by abundance and species richness of natural enemy communities (Dainese et al., 2019; Snyder, 2019). In contrast, we know much less about the effects of natural enemy evenness on natural pest control effectiveness (Snyder, 2019). Studies have found contrasting results that range from positive (Crowder et al., 2010; Mace and Mills, 2017; Yuan et al., 2019), neutral (Mace and Mills, 2017; Rusch et al., 2015) and negative (Dainese et al., 2019) relationships between natural enemy evenness and pest control effectiveness. These inconsistent response patterns can be explained by different mechanisms. Regarding the positive relationship, Snyder (2019) suggested that higher evenness can guarantee that each ecological niche can be occupied more completely, therefore, different species of natural enemies can better complement each other. Crowder et al. (2010) found that higher evenness reduced intraguild interferences which helped promote the aphid suppression efficiency. Oppositely, Hillebrand et al. (2008) argued that the efficiency of a community to provide the ecosystem services is determined by the proportion of the species that most efficiently provide the ecosystem services. This would indicate that the service provisioning efficiency is determined by the abundance of the most efficiency species and such mechanisms have been demonstrated for pollination services and pollinators (Winfree et al., 2015). If this mechanism predominantly shapes pest control services, higher evenness may reduce the relative abundance of the most efficient species thus resulting in a negative relationship between natural enemy evenness and pest suppression effectiveness (Dainese et al., 2019).

In Chapter 5, a cage experiment was carried out in which aphids were exposed to natural enemy communities that had the same abundance and species richness but differed in evenness. This design allowed to separate the effects of natural enemy evenness from the effects of other community metrics like abundance or species richness. The results suggested a causal positive relationship between natural enemy evenness and pest suppression effectiveness. However, the results of this study also showed that the effect of natural enemy evenness on pest suppression was less pronounced than that of abundance of lady beetles. These results indicated that the effect of evenness is context dependent and can easily be obscured by other natural enemy community characteristics like abundance and species richness in real agroecosystems, which could partly explain why management practices aiming at promoting abundance of natural enemies often have mixed effects on pest control. Nevertheless, increasing evenness will result in straight-forward increases in pest control with possible associated benefits to community resilience and stability (Wittebolle et al., 2009; Wan et al., 2014). Evenness is therefore an important component contributing to the functioning of natural enemy communities and the services they provide.

In real-world agricultural production, enhancing soil organic matter could be a feasible way to enhance arthropod evenness (Aldebron et al., 2020). In Chapter 3, I also found support that higher soil organic carbon content promoted the activity density of non-dominant carabid beetles, which resulted in a positive (but non-significant) trend between soil organic carbon content and evenness of total carabid beetles. Soils with higher organic matter content can provide additional food resources and helps to shape more complex soil structure (Bulluck III et al., 2002; Birkhofer et al., 2008). These additional resources can create additional ecological niches that accommodate more arthropod natural enemies and mediate intraguild inferences (Snyder, 2019; Snyder et al., 2022). Since intensive agricultural production practices are causing soil organic matter loss worldwide (Smith, 2008; Stockmann et al., 2015), understanding the effects of soil organic matter in biodiversity conservation and ecosystem services provisioning can provide more arguments to take actions to maintain or restore soil organic matter.

Concluding remarks and future directions

In this thesis, I have provided a comprehensive overlook on how multiple natural enemy guilds respond to multiple environmental factors at different spatial scales. I found that different natural enemy guilds responded inconsistently to agricultural intensification. This finding partly explains why conservation practices aiming at promoting one natural enemy guild may adversely decrease another guild and finally failed to enhance overall natural pest control services (Tscharntke et al., 2016; Karp et al., 2018). The inconsistent response patterns also demonstrate that some species of natural enemies have adapted well to the disturbance caused by human agricultural production and these species can persist or even increase in highly-intensified agricultural landscapes. This finding highlights the resilience of natural enemy communities to agricultural intensification. These well-adapted natural enemy species can guarantee the stability of ecosystem services delivery to a certain degree (Kleijn et al., 2015). However, this finding is not an argument to ignore the negative effects of current agricultural production methods on natural enemies as there are certainly limits to the resilience of natural enemy communities and beyond these limits changes could result in loss of function. This finding highlights the importance of conservation strategies to distinguish between the species that are well-adapted to and the species that are negatively affected by agricultural intensification and expansion. Furthermore, I found the importance of quantity and quality of semi-natural habitats in supporting natural enemy diversity, which suggests that measures to conserve agrobiodiversity are most effective when they are implemented at multiple spatial scales (Tscharntke et al., 2005).

An underlying motivation of this thesis is to better understand how environment, natural enemy community diversity and composition, and natural pest control services are interlinked, so that it is possible to formulate clearer and more feasible ecological intensification practices that are acceptable for agricultural sector. The agricultural sector is facing the challenge to produce enough food while maintaining agrobiodiversity (Kremen and Merenlender, 2018). This thesis found that these two challenges are not always mutually exclusive and can be sometimes be reconciled. Improving available resources of semi-natural habitats by establishing wildflower strips on field margins has been proven to be an effective way in enhancing abundance or diversity of natural enemies, natural pest control and crop yield (Tschumi et al., 2015; Tschumi et al., 2016b; Albrecht et al., 2020) but I found that such practices can be implemented more cost-effectively by managing pre-existing field margins by utilizing spontaneously emerging flowers. This measure could be more acceptable to farmers as they do not need to establish new wildflower strips and take land out of production. Another effective way could be to improve soil organic matter content in fields. A higher soil organic matter content can provide additional resources like food and shelter for ground-active arthropods and these resources are particularly essential for non-dominant natural enemies which can help to enhance community evenness (Aldebron et al., 2020). Since enhancing soil organic matter has also been suggested as an effective way to stabilize or bolster agricultural productivity (Pan et al., 2009; Oldfield et al., 2019; Kane et al., 2021), measures aiming at enhancing soil organic matter in fields could be regarded as a win-win solution for agricultural sector.

This thesis has provided some concrete suggestions for farmers to better implement practices proposed by ecological intensification. However, I did not evaluate the exact economic costs and benefits of such measures. For farmers, the net economic benefits are one of the most fundamental motivations to change farm management and implement practices proposed by ecological intensification (Kleijn et al., 2019). To better convince farmers to adopt these measures, calculating the trade-offs from an economic perspective represents an important topic for future research.

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Summary

Agricultural production relies fundamentally on ecosystem services and the majority of these services are provided by species that occur naturally in agricultural landscapes. However, the transition of traditional agricultural production to intensified agricultural production has negatively impacted the environment and severely threatened agrobiodiversity, thus weakening the associated ecosystem service delivery. Ecological intensification has been proposed as a solution to promote current high-input agriculture to become more sustainable. Ecological intensification aims at promoting ecosystem services by better conserving the species which provide these services. That way agricultural productivity can be maintained or even improved ultimately resulting in a win-win situation where agrobiodiversity conservation and food security can be simultaneously achieved. To better help the agricultural sector to implement ecological intensification, we need to better understand how different service providers respond to surrounding environmental factors or field management practices and how the characteristics of service-providing communities affect the efficiency of final service delivery. Natural pest control represents an important regulating service and studies examining how natural pest control interlinks with environmental factors or natural enemy diversity are increasing rapidly. However, natural enemies are from a wide range of orders or families with contrasting ecological traits or life histories. Complex intraguild natural enemy interferences are known to happen. As a result, there is still no clear framework for landscape and local scale drivers of natural pest control service delivery. This thesis examined how multiple natural enemy species groups are affected by environmental factors at different spatial scales, and how the efficiency of natural pest control delivery is affected by the community evenness and composition of natural enemies. This thesis contributes to the evidence base of ecological intensification by showing that under certain conditions enhancing natural pest control services and conserving agrobiodiversity are compatible objectives in agricultural landscapes.

In Chapter 2, we first examined how wildflower strips, a practice that is widely advocated by the academic sector but seldomly implemented by farmers, affect the abundance of natural enemies, natural pest control service and crop yield. We furthermore examined the effects of floral resources in field margins rather than wildflower strip establishment per se and how the effects of the floral resources on natural enemy abundance, natural pest control service and crop yield were affected by on-field management. We found that presence of wildflower strips did not affect ground-dwelling natural enemies, aphids or crop yield. However, flower availability across wildflower strips and control margins was positively related to the abundance of the pooled number of examined natural enemies, spiders and carabid beetles, and wheat yield. Positive effects in the crop fields were observed over limited distances; up to 5 m from the edge for spiders and wheat yield. The effects of flower availability and on-field management practices on natural enemies, aphids and wheat yield did not interact suggesting that, in our study, the effects of flowers were not influenced by insecticide or fertilizer applications but were mainly additive. This suggests that cover and richness of wildflowers in field margin habitat, rather than establishment of wildflower strips per se, drove increases in natural enemies and crop yield. Therefore, more attention should be given to the optimization of the establishment success of seed mixtures and to management practices enhancing wildflower cover and diversity which could represent a more cost-effective way to boost ecosystem services.

In Chapter 3, we carried out a meta-analysis across four countries in north-western Europe. We used carabid beetles and spiders as bioindicators and examined how their abundance, species richness and evenness were jointly affected by crop yield (as a proxy of local land-use intensity), percentage cropland (a proxy for landscape complexity) and soil organic carbon content, and whether these patterns differed between nationally dominant and non-dominant species (whether carabid beetle or spider species made up respectively more or less than 5% of the total number of individuals caught of each species group in a country). We found that the majority of the individuals of both carabid beetles and spiders were from the dominant species. Less than 17% of carabid or spider species were classified as dominant, which accounted for more than 90% of individuals respectively. Furthermore, we found that carabids and spiders were generally related to different aspects of agricultural intensification. Carabid species richness was positively related with crop yield and evenness was negatively related to crop cover. The activity density of non-dominant carabids was positively related with soil organic carbon content. Meanwhile, spider species richness and non-dominant spider species richness and activity density were all negatively related to percentage cropland. The inconsistent response patterns between the two guilds indicate that practices targeted to enhance one functionally important guild may not promote another key guild, which helps explain why conservation measures to enhance natural enemies generally often do not enhance pest regulation. We found that the response patterns of dominant and non-dominant species were generally similar, which suggests that management practices to enhance service provisioning by a certain guild can also enhance the overall diversity of that particular guild.

In Chapter 4, using the same data as Chapter 3, we examined how β-diversity of carabid beetles and spiders was affected by distance on one hand and crop yield, the percentage cropland and the soil organic carbon content on the other. We found that 55% and 75% of all observed carabid and spider individuals, respectively, belonged to species that occurred in all four countries. However, individuals of nationally unique species only accounted for 3% of all individuals for both guilds. Furthermore, we only found a negative relationship between distance and similarity of spider communities but not for carabid beetle communities. None of the environmental variables were related to the similarity of carabid beetle and spider communities, or moderated the effects of distance. Our study indicates that across a significant part of the European continent, arthropod communities (especially carabid beetles) in agricultural landscapes are composed of very similar species that are apparently robust to environmental change.

In Chapter 5, we explored the underlying mechanisms of how natural enemy evenness and composition affected natural pest control. We carried out a control experiment that exposed *Sitobion avenae* aphid colonies in experimental cages to natural enemy communities that had the same abundance and species richness but that differed in evenness and dominant species. We found that the identity of the most dominant species in the arthropod predator community predominantly drove the pest control efficiency. However, in addition to the effects of species identity, we also found a causal positive relationship between the evenness of arthropod predator communities and the suppression of pest population growth. Our results provide support for the hypothesis that ecosystem service provision is generally a function of the abundance and efficiency of the most dominant species of the service-providing groups. This could partly explain why management practices aiming at promoting abundance of natural enemies often have mixed effects on pest control. Our results also demonstrate that diversity components such as evenness can have important additional effects. However, in real-world ecosystems, these effects may be obscured because evenness is generally confounded with abundance or species richness in natural enemy predator communities.

The results of these studies show that different guilds of natural enemies displayed inconsistent responses to agricultural intensification. This highlights the importance for strategies to enhance natural enemy communities to first distinguish between the well-adapted species and the species that are negatively affected by agricultural intensification and expansion. More specific measures are probably required to promote the more vulnerable species. Furthermore, quality and quantity of non-crop elements are important for arthropod natural enemies in agricultural landscapes, which highlights the importance to take conservation measures at multiple spatial scales. Besides, we found that the efficiency of natural pest control is predominantly determined by the relative abundance of the most efficient species but higher evenness can additionally enhance natural pest control. These studies confirmed that agrobiodiversity conservation and ecosystem services delivery can, under the right conditions, be compatible objectives in agricultural landscapes. However, more social and economic considerations are required before we are in a position to convince the agricultural sector to adopt ecological intensification practices.

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About the author

Zulin Mei was born on April 28, 1994, in Guizhou, China. His hometown, surrounded by the natural beauty of trees, rivers, and mountains, played a significant role in shaping his deep passion for nature. During his early years, Zulin's parents regularly took him to explore the wonders of nature, laying the foundation for his enduring connection to the environment and inspiring his academic journey.

In 2012, he embarked on his academic pursuits by enrolling in the Bachelor of Ecology at China Agricultural University. His initial interest in nature evolved into a focused pursuit aimed at understanding the underlying ecological mechanisms.

Continuing his academic journey, Zulin pursued a master's degree in landscape ecology at the same university from 2016. Under the guidance of Prof. Zhenrong Yu and Prof. Yunhui Liu, his research delved into understanding how carabid beetles and spiders respond to varying habitats in agricultural landscapes at different altitudes.

In 2018, Zulin's academic journey took an international turn as he secured a position as PhD student in the Plant Ecology and Nature Conservation Group at Wageningen University in the Netherlands. Under the supervision of Prof. David Kleijn and Dr. Jeroen Scheper, his research focused on investigating the relationships between environmental factors and natural enemies and natural pest control. After a committed five-year journey of scholarly exploration, the fruition of this doctoral endeavor now unfolds before you….

List of Publications

Published papers

Mei, Z., de Groot, G. A., Kleijn, D., Dimmers, W., van Gils, S., Lammertsma, D., ... & Scheper, J. (2021). Flower availability drives effects of wildflower strips on ground-dwelling natural enemies and crop yield (**Chapter 2** of this thesis). Agriculture, Ecosystems & Environment, 319, 107570.

Mei, Z., Scheper, J., Bommarco, R., de Groot, G. A., Garratt, M. P., Hedlund, K., ... & Kleijn, D. (2023). Inconsistent responses of carabid beetles and spiders to land-use intensity and landscape complexity in north-western Europe (**Chapter 3** of this thesis). Biological Conservation, 283, 110128.

Mei, Z., Scheper, J., & Kleijn, D. (2023). Arthropod predator identity and evenness jointly shape delivery of pest control services (**Chapter 5** of this thesis). Pest Management Science.

Hu, W., **Mei, Z.**, Liu, Y., Yu, Z., Zhang, F., & Duan, M. (2022). Recovered grassland area rather than plantation forest could contribute more to protect epigeic spider diversity in northern China. Agriculture, Ecosystems & Environment, 326, 107726.

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Under review

Mei, Z., Scheper, J., Bommarco, R., de Groot, G. A., Garratt, M. P., Potts, S. G., ... & Kleijn, D. Distance decay effects predominantly shape spider but not carabid community composition in crop fields in north-western Europe (**Chapter 4** of this thesis). Submitted to Basic and Applied Ecology

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Zulin Mei (梅祖麟) on 22-11-2023 in Wageningen

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 30 ECTS (= 22 weeks of activities)

Review/project proposal (9 ECTS)

- The relationship between land use intensity and diversity and evenness of natural enemies and natural pest control

Post-graduate courses (5.1 ECTS)

- Consumer resource interactions; PE&RC (2018)
- Basic statistics; PE&RC (2018)
- Introduction to R for statistical analysis; PE&RC (2019)
- Bugs at your service; PE&RC (2019)

Laboratory training and working visits (0.1 ECTS)

- Get to know the work of dietary industry on sustainability: career after PhD; Friesland Campina (2023)

Invited review of journal manuscripts (1 ECTS)

- Journal of Applied Entomology: field margins and cropping system influence diversity and abundance of aphid natural enemies in *Lablab purpureus* (2022)

Competence, skills and career-oriented activities (3.5 ECTS)

- Reviewing a scientific manuscript; WGS (2019)
- Scientific writing; Wageningen in'to languages (2021)
- Last stretch of the PhD programme; WGS (2022)
- Writing propositions for your PhD; WGS (2022)
- Career perspectives; WGS (2023)

Scientific integrity/ethics in science activities (0.3 ECTS)

- Ethics in plant and environmental sciences; WGS (2019)

PE&RC Annual meetings, seminars and the PE&RC retreat (2.7 ECTS)

- PE&RC Day (2018, 2019, 2023)
- PE&RC Weekend first year (2019)
- PE&RC Event midterm (2021)
- PE&RC Retreat last year (2022)

Discussion groups/local seminars or scientific meetings (6.8 ECTS)

- Symposium innovation for conservation: pushing technological frontiers (2019)
- Symposium towards ecological intensification (2019)
- An introduction to LaTeX (2020)
- Wageningen evolution and ecology seminars (2022-2023)
- Biodiversity in agroecosystems (2022-2023)
- Agroecology and ecological intensification: perspectives from Europe and Latin America (2023)
- Current themes optimizing ecological structure to enhance biodiversity and genetic vitality (2023)

International symposia, workshops and conferences (3.2 ECTS)

- Netherlands annual ecology meeting; oral presentation; online (2021)
- Netherlands annual ecology meeting; poster presentation; Lunteren, the Netherlands (2022)

Colophon

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