Opportunities and obstacles of ecological intensification:
Biological pest control in arable cropping systems

Chancen und Hürden Ökologischer Intensivierung:
Biologische Schädlingsbekämpfung im Ackerbau

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Dissertation zur Erlangung des naturwissenschaftlichen Doktorgrades
Julius-Maximilians-Universität Würzburg

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geboren in Lörrach

Würzburg, 2018

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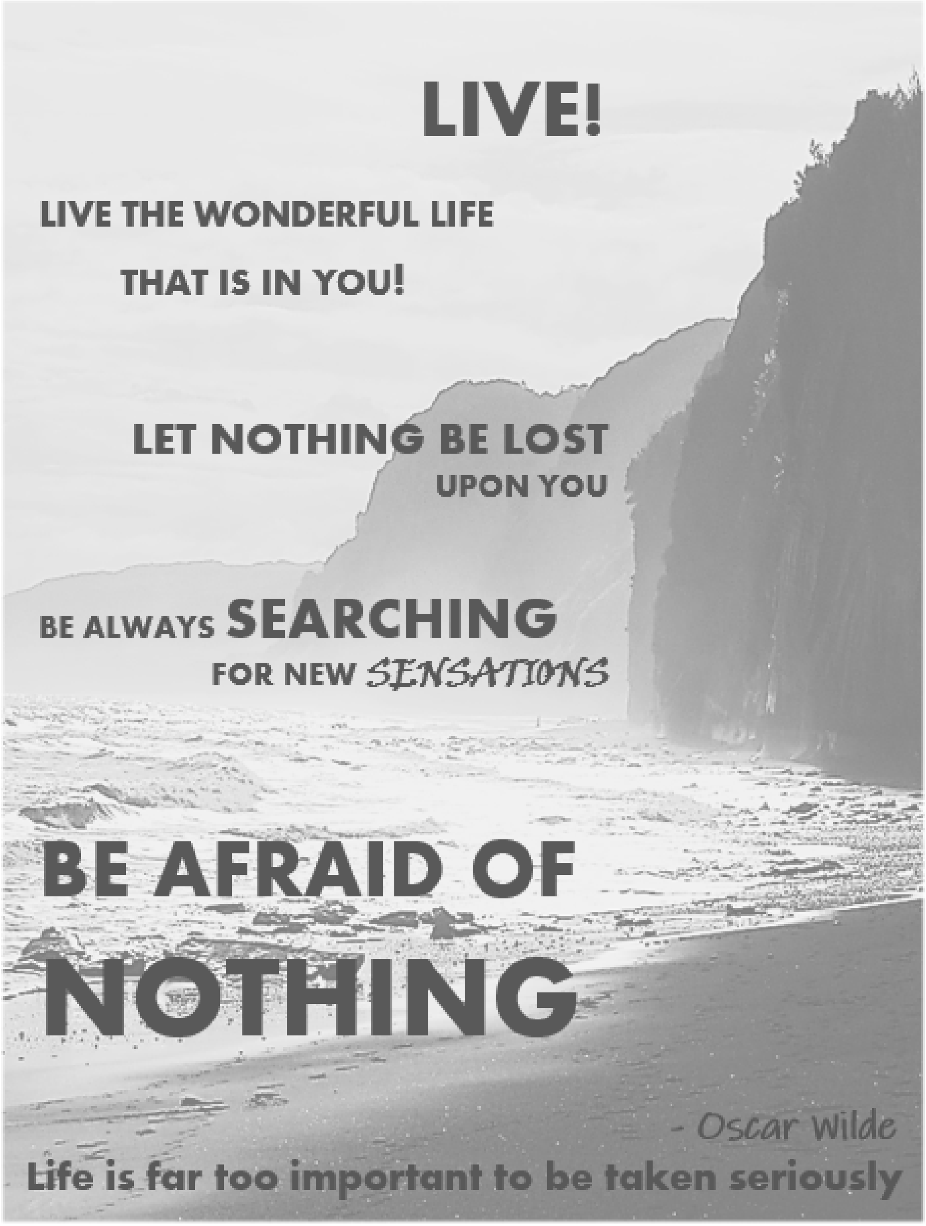
Date of Receipt of Certificates/Doktorurkunde ausgehändigt am:



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LIVE THE WONDERFUL LIFE
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LET NOTHING BE LOST
UPON YOU

BE ALWAYS **SEARCHING**
FOR NEW *SENSATIONS*

BE AFRAID OF
NOTHING

- Oscar Wilde

Life is far too important to be taken seriously

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Summary

Chapter I – General introduction

Modern agriculture is the basis of human existence, a blessing, but also a curse. It provides nourishment and well-being to the ever-growing human population, yet destroys biodiversity-mediated processes that underpin productivity: ecosystem services such as water filtration, pollination and biological pest control. Ecological intensification is a promising alternative to conventional farming, and aims to sustain yield and ecosystem health by actively managing biodiversity and essential ecosystem services. Here, I investigate opportunities and obstacles for ecological intensification. My research focuses on 1) the relative importance of soil, management and landscape variables for biodiversity and wheat yield (Chapter II); 2) the influence of multi-scale landscape-level crop diversity on biological pest control in wheat (Chapter III) and 3) on overall and functional bird diversity (Chapter IV). I conclude 4) by introducing a guide that helps scientists to increase research impact by acknowledging the role of stakeholder engagement for the successful implementation of ecological intensification (Chapter V).

Chapter II - Ecological pathways to high yields in conventional cereal systems

Ecological intensification relies on the identification of natural pathways that are able to sustain current yields. Here, we crossed an observational field study of arthropod pests and natural enemies in 28 real-life wheat systems with an orthogonal on-field insecticide-fertilizer experiment. Using path analysis, we quantified the effect of 34 factors (soil characteristics, recent and historic crop management, landscape heterogeneity) that directly or indirectly (via predator-prey interactions) contribute to winter wheat yield. Reduced soil preparation and high crop rotation diversity enhanced crop productivity independent of external agrochemical inputs. Concurrently, biological control by arthropod natural enemies could be restored by decreasing average field sizes on the landscape scale, extending crop rotations and reducing soil disturbance. Furthermore, reductions in agrochemical inputs decreased pest abundances, thereby facilitating yield quality.

Chapter III - Landscape-level crop diversity benefits biological pest control

Landscape-level crop diversity is a promising tool for ecological intensification. However, biodiversity enhancement via diversification measures does not always translate into agricultural benefits due to antagonistic species interactions (intraguild predation). Additionally, positive effects of crop diversity on biological control may be masked by inappropriate study scales or correlations with other landscape variables (e.g. seminatural habitat). Therefore, the multiscale and context-dependent impact of crop diversity on biodiversity and ecosystem services is ambiguous. In 18 winter wheat fields along a crop diversity gradient, insect- and bird-mediated pest control was assessed using a natural enemy exclusion experiment with cereal grain aphids. Although birds did not influence the strength of insect-mediated pest control, crop diversity (rather than seminatural habitat cover) enhanced aphid regulation by up to 33%, particularly on small spatial scales. Crop diversification, an important Greening measure in the European Common Agricultural Policy, can improve biological control, and could lower dependence on insecticides, if the functional identity of crops is taken into account. Simple measures such as 'effective number of crop types' help in science communication.

Chapter IV - Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes

Although avian pest control did not respond to landscape-level crop diversity, birds may still benefit from increased crop resources in the landscape, depending on their functional grouping (feeding guild, conservation status, habitat preference, nesting behaviour). Observational studies of bird functional diversity on 14 wheat study fields showed that non-crop landscape heterogeneity rather than crop diversity played a key role in determining the richness of all birds. Insect-feeding, non-farmland and non-threatened birds increased across multiple spatial scales (up to 3000 m). Only crop-nesting farmland birds declined in heterogeneous landscapes. Thus, crop diversification may be less suitable for conserving avian diversity, but abundant species benefit from overall habitat heterogeneity. Specialist farmland birds may require more targeted management approaches.

Chapter V - Growing TREEs for a sustainable future – a guide to the implementation of ecological farming

Identifying ecological pathways that favour biodiversity and ecosystem services provides opportunities for ecological intensification that increase the likelihood of balancing conservation and productivity goals. However, change towards a more sustainable agriculture will be slow to come if research findings are not implemented on a global scale. During dissemination activities within the EU project Liberation, I gathered information on the advantages and shortcomings of ecological intensification and its implementation. Here, I introduce a guide ('TREE') aimed at scientists that want to increase the impact of their research. TREE emphasizes the need to engage with stakeholders throughout the planning and research process, and actively seek and promote science dissemination and knowledge implementation. This idea requires scientists to leave their comfort zone and consider socioeconomic, practical and legal aspects often ignored in classical research.

Chapter VI – General discussion

Ecological intensification is a valuable instrument for sustainable agriculture. Here, I identified new pathways that facilitate ecological intensification. Soil quality, disturbance levels and spatial or temporal crop diversification showed strong positive correlations with natural enemies, biological pest control and yield, thereby lowering the dependence on agrochemical inputs. Differences between functional groups caused opposing, scale-specific responses to landscape variables. Opposed to our predictions, birds did not disturb insect-mediated pest control in our study system, nor did avian richness relate to landscape-level crop diversity. However, dominant functional bird groups increased with non-crop landscape heterogeneity. These findings highlight the value of combining different on-field and landscape approaches to ecological intensification. Concurrently, the success of ecological intensification can be increased by involving stakeholders throughout the research process. This increases the quality of science and reduces the chance of experiencing unscalable obstacles to implementation.

Zusammenfassung

Kapitel I – Allgemeine Einführung

Die moderne Landwirtschaft ist die Grundlage menschlichen Lebens, ein Segen, aber auch ein Fluch. Sie stellt Nahrung und Wohlstand für die immerfort wachsende menschliche Bevölkerung bereit, und zerstört gleichzeitig Biodiversitäts-geförderte Prozesse, welche die Produktivität unterstützen: Ökosystemdienstleistungen wie Wasseraufbereitung, Bestäubung und biologische Schädlingsbekämpfung. Ökologische Intensivierung ist eine vielversprechende Alternative zur konventionellen Landwirtschaft, und zielt darauf aus, Erträge und die Gesundheit von Ökosystemen zu erhalten indem Biodiversität und essentielle Ökosystemdienstleistungen aktiv gemanagt werden. In meiner Doktorarbeit untersuche ich die Chancen und Hürden Ökologischer Intensivierung. Das Hauptinteresse meiner Forschung liegt bei 1) der relativen Bedeutung von Boden, Bewirtschaftung und Landschaftsaspekten für Biodiversität und Weizenerträge (Kapitel II); 2) dem Einfluss regionaler Anbauvielfalt auf verschiedenen räumlichen Skalen auf die biologische Schädlingsbekämpfung in Weizen (Kapitel III) und 3) auf die gesamte und funktionelle Artenvielfalt von Vögeln (Kapitel IV). Zum Schluss 4) stelle ich einen Leitfaden vor, der Wissenschaftlern hilft die Wirkung ihrer Forschung zu erhöhen, indem die fundamentale Rolle von Stakeholdern für die Umsetzung Ökologischer Intensivierung besser genutzt wird (Kapitel V).

Kapitel II – Ökologische Wege zu hohen Erträgen in konventionellen Getreide Anbausystemen

Ökologische Intensivierung bedarf der Identifizierung von natürlichen Prozessen, die zum Erhalt landwirtschaftlicher Erträge beitragen. Zu diesem Zweck verknüpften wir eine Beobachtungsstudie, in der Schädlinge und natürliche Gegenspieler in 28 realen Weizen Anbausystem aufgenommen wurden, mit einem orthogonalen Feldexperiment (Insektizid und mineralische Düngung). Anhand einer Pfadanalyse quantifizierten wir den Einfluss von 34 Faktoren (Bodencharakteristiken, gegenwärtige und vergangene Bewirtschaftung, Landschaftsheterogenität), die direkt oder indirekt (über Räuber-Beute-

Interaktionen) Einfluss auf den Winterweizenertrag ausüben. Reduzierte Bodenbearbeitung und vielfältige Fruchtfolgen erhöhten die Erträge unabhängig von der Ausbringung von Agrochemikalien. Gleichzeitig könnte die biologische Schädlingsbekämpfung durch räuberische Insekten wiederhergestellt werden, indem durchschnittliche Schlaggrößen auf der Landschaftsebene verringert, Fruchtfolgen erweitert und die Bodenbearbeitung reduziert wird. Des Weiteren senkte der Verzicht auf Agrochemikalien das Schädlingsaufkommen einiger Arten, und trug zu einer höheren Ertragsqualität bei.

Kapitel III – Regionale Anbauvielfalt erhöht die biologische Schädlingsbekämpfung

Regionale Anbauvielfalt ist ein vielversprechendes Mittel zur Ökologischen Intensivierung. Doch die Erhöhung der Artenvielfalt durch Diversifizierungsmaßnahmen führt nicht immer zu Vorteilen in der Landwirtschaft, vor allem auf Grund antagonistischer Wechselwirkungen zwischen verschiedenen Arten (intraguild predation). Weiterhin können positive Effekte der Anbauvielfalt durch die Wahl der falschen räumlichen Skala oder durch Korrelationen mit anderen Landschaftsvariablen (z.B. halbnatürliche Habitate) überdeckt werden. Aus diesem Grund bestehen Unklarheiten über die Wirkung von Anbauvielfalt auf Biodiversität und Ökosystemdienstleistungen in unterschiedlichen räumlichen Skalen und Kontexten. Durch Ausschlussexperimente mit Getreideblattläusen untersuchten wir die biologische Schädlingsbekämpfung durch räuberische Insekten und Vögel in 18 Winterweizenfeldern innerhalb eines Landschaftsgradienten der Anbauvielfalt. Vögel hatten keinen Einfluss auf die biologische Schädlingsbekämpfung durch Insekten. Anbauvielfalt (nicht das Vorkommen halbnatürlicher Habitate) erhöhte die Schädlingsbekämpfung um bis zu 33%, vor allem auf kleinen räumlichen Skalen. Somit kann die Steigerung der Anbauvielfalt, eine wichtige Säule der Europäischen Gemeinsamen Agrarpolitik, die biologische Schädlingsbekämpfung verbessern und den Einsatz von Agrochemikalien verringern, solange die funktionelle Gruppe der Anbaupflanzen berücksichtigt wird. Einfache Maßeinheiten wie die ‘effektive Anzahl an

Kulturpflanzengruppen‘ helfen in der Kommunikation wissenschaftlicher Ergebnisse.

Kapitel IV – Landschaftsheterogenität nicht Anbauvielfalt bestimmen die Vogelvielfalt in Agrarlandschaften

Obwohl die Schädlingsbekämpfung durch Vögel nicht durch regionale Anbauvielfalt beeinflusst wurde, könnten Vögel, abhängig von der Zugehörigkeit zu bestimmten funktionellen Gruppen (Ernährung, Gefährdungsstatus, Lebensraum, Nistplatzwahl), dennoch von erhöhten Ressourcen auf landwirtschaftlichen Flächen profitieren. In einer Beobachtungsstudie wurde die funktionelle Vielfalt von Vögeln auf 14 Winterweizenfeldern aufgenommen. Die Studie zeigte, dass die nicht agrarisch genutzte Landschaftsheterogenität im Vergleich zur regionalen Anbauvielfalt eine übergeordnete Rolle für die Artenvielfalt spielte, vor allem für Insektenfresser, Vögel die außerhalb landwirtschaftlicher Flächen siedeln oder nicht in ihrem Bestand gefährdet sind. Effekte waren auf allen Skalen sichtbar (bis zu 3000m). Nur Acker-nistende Agrarvögel zeigten negative Beziehungen zu Landschaftsheterogenität. Der Nutzen der Anbaudiversifizierung scheint weniger Bedeutung für den Vogelschutz zu haben als die übergeordnete Vielfalt der Landschaft, welche den Artenreichtum häufiger Vogelarten erhöhte. Spezialisierte Vogelarten dagegen bedürfen eines gezielten, angepassten Managements.

Kapitel V - Bäume (TREEs) pflanzen für eine nachhaltige Zukunft – ein Leitfaden zur Umsetzung Ökologischer Intensivierung

Um Ökologische Intensivierung voranzutreiben und ein Gleichgewicht zwischen Naturschutz- und Produktivitätszielen zu erreichen, bedarf es der Identifikation ökologischer Prozesse, die zur Steigerung von Biodiversität und Ökosystemdienstleistungen beitragen. Doch der die Wende zu einer nachhaltigeren Landwirtschaft wird nur langsam voran schreiten, wenn Forschungsergebnisse nicht global umgesetzt werden. Während der Öffentlichkeitsarbeit im EU Projekt Liberation konnte ich Informationen über die Vor- und Nachteile Ökologischer

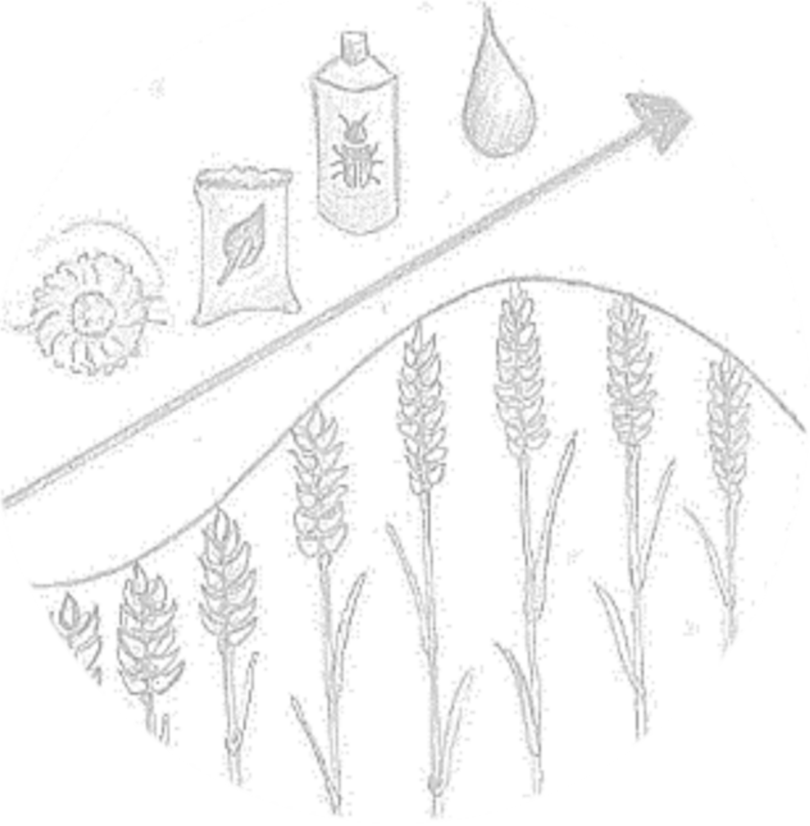
Intensivierung und deren Umsetzung sammeln. Hier stelle ich einen Leitfaden ('TREE') vor, der Wissenschaftlern helfen soll die Wirkung ihrer Forschung zu erhöhen. TREE verdeutlicht wie wichtig es ist, Stakeholder in den Planungs- und Forschungsprozess eines Projektes mit einzubeziehen, und aktiv die Verbreitung von Wissen und die Umsetzung wissenschaftlicher Ergebnisse voranzutreiben. TREE fordert Wissenschaftler dazu auf, die eigene Komfortzone zu verlassen und sozioökonomische, praktische und rechtliche Aspekte zu berücksichtigen, welche oft in der klassischen Forschung unbeachtet bleiben.

Kapitel VI – Allgemeine Diskussion

Ökologische Intensivierung ist ein bedeutender Schritt in Richtung nachhaltige Landwirtschaft. In dieser Arbeit identifiziere ich neue Wege zur ökologischen Intensivierung. Bodenqualität, Störungsgrad des Bodens und die räumliche oder zeitliche Anbauvielfalt zeigten starke positive Korrelationen mit natürlichen Gegenspielern, biologischer Schädlingsbekämpfung und Erträgen auf, wodurch die Abhängigkeit von Agrochemikalien verringert wird. Unterschiede zwischen funktionellen Gruppen verursachten gegensätzliche Beziehungen zu Landschaftsvariablen auf verschiedenen räumlichen Skalen. Entgegen unserer Erwartungen nahmen Vögel in unserem System keinen Einfluss auf die biologische Schädlingsbekämpfung durch Insekten. Die Vogelvielfalt war außerdem unbeeinflusst von der regionalen Anbauvielfalt. Doch dominante funktionelle Vogelgruppen profitieren von der Vielfalt nicht agrarisch genutzter Landschaftsaspekte. Diese Ergebnisse betonen den Wert einer Mischung aus unterschiedlichen lokalen und landschaftsbezogenen Ansätzen zur Ökologischen Intensivierung. Gleichzeitig kann der Erfolg Ökologischer Intensivierung vor allem dadurch erhöht werden, dass Stakeholder in den Forschungsprozess eingebunden werden. Dies steigert die Qualität der Forschung und reduziert die Wahrscheinlichkeit, während der Umsetzung auf unüberwindbare Hürden zu stoßen.

Chapter I

General Introduction



Agriculture plays an integral role in the history of human civilization, as it builds the foundation of population growth, wealth and well-being. At the same time, however, intensive agricultural practices threaten the stability and resilience of natural ecosystems, as biodiversity and associated ecosystem services are eroded. Humanity faces the challenge of drastically changing the ways in which food is produced, or suffering from the long-term negative consequences, if natural resources and ecological processes are deteriorated beyond repair. Using ecological theories and knowledge of traditional farming systems, researchers investigate alternative ways of farming that could increase the sustainability of modern agriculture. One such approach is ecological intensification, which actively manages on- and off-farm biodiversity to enhance essential ecosystem services such as nutrient cycling, pollination and biological pest control. The EU-funded project Liberation (LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensification) aimed to provide the evidence base for ecological intensification. Within this framework I aimed to identify ecological pathways to ecological intensification. My research focused on 1) the relative effects of soil, management and landscape on biodiversity and yield in winter wheat (Chapter II), 2) the role of landscape-level crop diversity on the ecosystem service pest control (Chapter III) and overall and functional bird diversity (Chapter IV), and 4) obstacles and opportunities for implementing ecological intensification, based on numerous dissemination activities conducted within the project Liberation (Chapter V).

Agriculture /ˈæɡrɪkʌltʃə(r)/ *noun*
The science or practice of farming. Middle English adaptation of the Latin word *agricultūra,* from *ager* (field) and *cultura* (cultivation)

Oxford Dictionary 2018

I.1 Sculpting the earth with scythe and plough

The history of agriculture began with the unwillingness and inability of humankind to continue living as hunters and gatherers, chasing animal prey and relying on naturally grown resources to provide nourishment. So, in a gradual process starting around 10,000 years ago (Smith, 1998), humans settled. They tried themselves on cultivating and domesticating crops and livestock, thereby increasing the global carrying capacity that previously restrained population growth. While the benefits of agriculture were soon mirrored in human demography, the biggest break-through came with the green revolution starting in the 1960s, when global food productivity skyrocketed and undernourishment decreased due to the creation of high-yielding varieties of staple crops (wheat, rice, maize), technical advancement and agricultural intensification (Tilman *et al.*, 2002; Pingali, 2012). Today, agricultural production areas cover *c.* 40% of terrestrial land (Foley *et al.*, 2005) and provide us with the basis of human existence: agricultural products such as cereals, fruit, vegetables and meat. However, despite its benefits, the green revolution has come at a price, as social, environmental and ecological costs of intensive agriculture accumulate.

First gradually, almost unbeknownst, then (over the last decades) increasingly self-evident has agriculture and human ingenuity chiselled its marks onto the surface of the earth: it has turned heterogeneous, biodiverse landscapes into endless monocultures, and benign natural systems into pesticide- and nitrogen-laden artificial mass production areas (FAOSTAT, 2001; Tilman *et al.*, 2002; Foley *et al.*, 2005). It has also reshaped human culture, the way we live, affect and perceive nature. Urbanization has dramatically increased, idyllic small-scale subsistence agriculture has been replaced by large-scale industrial farming businesses. Landscape simplification, farm specialization and intensive agricultural practices have caused unprecedented environmental damage (e.g. nutrient overloading, erosion) and biodiversity losses (Benton *et al.*, 2003; Foley *et al.*, 2005). Biodiversity losses are particularly heavy for insects and farmland birds (Hallmann *et al.*, 2017; BirdLife International, 2018), which suffer from the decline in resource availability and habitat diversity.

The impacts of agriculture on the environment and biodiversity in itself beg the question whether it is the moral obligation of humankind (the causal factor of change) to mitigate and counteract these trends. Should we preserve global diversity for the enjoyment of future generations and in its own interest? Yet there is more at stake than the loss of species. Intensive agricultural practices influence essential ecosystem services provided by functional diversity, such as pollination, pest regulation and soil services (e.g. nutrient cycling) (Altieri, 1999; Millenium Ecosystem Assessment, 2005; Bianchi *et al.*, 2006). Worldwide, the annual value of these ecosystem services has been estimated as topping US$117 billion (US$19.6 billion for cropland), US$417 billion (US$33.6 billion for cropland), and US$17 trillion (no values for cropland available), respectively (Costanza *et al.*, 1997).

With biodiversity and ecosystem services threatened by intensive agriculture, trade-offs between environmental (biodiversity conservation, ecosystem health), economic (productivity) and social goals (food security, public health) are inevitable (Foley *et al.*, 2005; Birkhofer *et al.*, 2008; Kleijn *et al.*, 2011; Kremen & Miles, 2012; Seufert *et al.*, 2012). Benign, healthy ecosystems with copious amounts of natural habitat and limited or extensive agriculture harbor a high diversity of plant and animal taxa. In contrast, intensively managed, high-productivity regions with large amounts of agrochemical inputs, simple crop rotations, high levels of soil disturbance and lack of seminatural structures are likely to be species poor. Focusing on individual, economic benefits of farming, intensive agroecosystems offer the greatest rewards, but associated negative externalities are not restrained within farm boundaries, and extent across regions and society as a whole (Stoate *et al.*, 2001). Thus, the long-term direct (investment) and indirect (ecological, socioeconomic and environmental) costs of agricultural practices such as pesticide application often outweigh the perceived benefits for farmers and crop productivity, especially if considering expenses for externalities that cannot be accurately valued (Wilson & Tisdell, 2001; Pimentel, 2005). Nevertheless, humankind has become reliant on high-yielding agriculture to feed the ever growing human population and ward off recurrent food shortages. Accordingly, current research efforts focus on the development of alternative ways of farming able to maintain or enhance agricultural productivity while reducing environmental and ecological externalities.

I.2 Thinking outside the box

Underlying recent research efforts aimed at mitigating the negative effects of agricultural intensification are two approaches that are opposing means to the same end: land-sparing vs. land-sharing (Green *et al.*, 2005). In the first case, wildlife-friendly farming (conservation of natural habitat, extensive management of seminatural habitat, and reduction of fertilizer and pesticide inputs) favours wildlife, yet often depresses yields (Rosenzweig, 2003). Considering the growing demand for food, this may require further conversion of natural habitats for agriculture, although species of conservation concern are often limited even on extensive cropland. In the land-sparing approach, yields on existing cropland are increased to compensate for yield losses resulting from habitat restoration efforts (Green *et al.*, 2005). In the end, the greatest likelihood of achieving a positive balance of productivity and conservation goals may be positioned somewhere in the middle between the land-sharing and land-sparing continuum, as demonstrated by 'ecological intensification' (Figure I.1). Ecological intensification aims to minimize external inputs and enhance agricultural sustainability by actively managing biodiversity and yield-supporting ecosystem services (Doré *et al.*, 2011; Bommarco *et al.*, 2013; Pywell *et al.*, 2015; Gurr *et al.*, 2016). Its success depends on the identification of ecological pathways that enhance productivity, and on the thorough assessment of their effectiveness. This generally requires researchers and practitioners alike to think outside the box, to delve into practical aspects of farming or extend their horizon beyond the field boundary, respectively. This has uncovered a range of on- and off-field factors that enhance biodiversity, ecosystem services and, in numerous cases, yields.

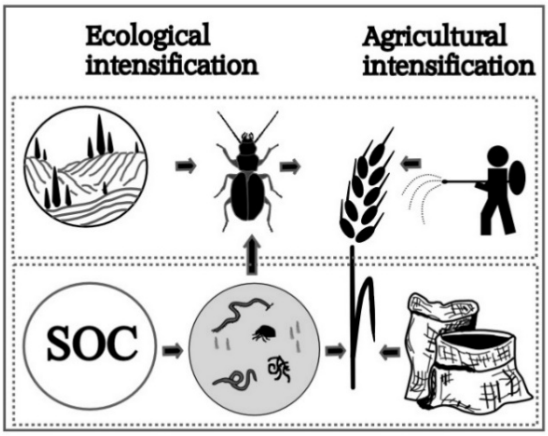


Figure I.1 Ecological intensification (left) enhances biodiversity and associated ecosystem services such as biological pest control and soil fertility via beneficial landscape and management aspects. This allows for the reduction of practices (e.g. pesticide and fertilizer application) associated with agricultural intensification (right). Graphic © Liberation

I.2.1 On-field pathways to ecological intensification

As the intensity of agricultural management is a key determinant of biodiversity, it stands to reason that various tools of ecological intensification rely on the adaption of management processes. This includes, *inter alia*, the amount of agrochemical inputs, soil and crop management regimes and field diversification practices.

Agrochemical inputs play a vital role in productivity growth, yet concurrently (and unintentionally) cause environmental change and biodiversity declines. For instance, mineral fertilization attracts pests to fields by enhancing crop quality, and detrimentally affects some soil-dwelling, predatory insects (Birkhofer *et al.*, 2008; Garratt *et al.*, 2011). Spraying of herbicides and insecticides may reduce pollination and biological pest control by affecting non-target beneficial organisms, with negative follow-on effects for productivity and higher trophic levels (Birkhofer *et al.*, 2008; Geiger *et al.*, 2010; Brittain & Potts, 2011; Krauss *et al.*, 2011; Jonsson *et al.*, 2012). Moreover, the practice of mixing different substances for plant protection may further accelerate the negative impacts on plant and animal biodiversity by creating new, deadly chemical compounds. In contrast, the targeted culprits, be it pathogenic fungi, weeds or pests, often evade decimation by evolving resistances against fungicides, herbicides and insecticides, consequently lowering the utility of pesticide application (Gould *et al.*, 2018). Seed dressing with neonicotinoids only superficially lessens the influence of insecticides by locally and systemically acting on arthropod pests (Goulson, 2013). Studies show, that neonicotinoids accumulate in soils and travel through the food chain via herbivores, nectar or pollen, impairing or killing non-target predators and pollinators, and consequently decreasing yields (Goulson, 2013; Douglas *et al.*, 2015). Furthermore, direct or indirect consumption of these toxic chemicals causes mortality in vertebrates such as birds and mammals (Goulson, 2013; Hallmann *et al.*, 2014).

In light of the long list of externalities and future potential deficits in non-renewable resources required for the production of some agrochemicals, a reduction in their use seems unavoidable. Although this may in some cases translate to lower productivity, the long-term socioeconomic, ecological and environmental benefits outweigh the disadvantages. For instance, decreased mineral fertilizer and insecticide input can facilitate pollinators (Brittain & Potts, 2011), predators (Geiger *et al.*, 2010; Krauss *et al.*, 2011; Gagic *et al.*, 2017) and parasitism rates (Jonsson *et al.*, 2012), while at the same time lowering pest pressure and crop damage (Birkhofer *et al.*, 2008; Geiger *et al.*, 2010; Krauss *et al.*, 2011; Garratt *et al.*, 2018b). Vertebrates such as birds also benefit from reduced pesticide application (Filippi-Codaccioni *et al.*, 2010; Geiger *et al.*, 2010). Accordingly, adaptation of agrochemical input regimes offers ecological pathways for augmenting biodiversity, ecosystem services and productivity.

In addition to agrochemical inputs, unsustainable soil management in form of low organic carbon input or soil disturbance is a major driver of soil-related biodiversity declines. Apart from enhancing soil quality, nutrient availability, water retention and plant growth, soil organic carbon (SOC) plays a vital role in agricultural systems by sustaining detritivore communities that act as alternative prey for soil-dwelling predators throughout the year (Birkhofer *et al.*, 2008). However, ploughing alters the physical characteristics of the soil and speeds decomposition of soil organic matter (Tilman *et al.*, 2002). Hence predators and biological pest control benefit from farming practices that enhance SOC (organic farming and fertilization, (Kromp, 1999; Birkhofer *et al.*, 2008; von Berg *et al.*, 2010) and lower soil disturbance (reduced tillage (Kromp, 1999; Tamburini *et al.*, 2015, 2016)), as do farmland birds that either rely on insect prey or undisturbed on-field nesting sites (McLaughlin & Mineau, 1995). Additionally, soil characteristics such as soil pH and soil type define biodiversity and productivity, but farmers are mostly unable to control these variables.

Other crop management factors are directly influenced by the farmer's decision of how to manage her land within the limits and regulations set by agricultural policies and socioeconomic boundaries. Biodiversity and ecosystem services respond to current and historic aspects of crop management, including sowing date and density of crops (Ozturk *et al.*, 2006; Valério *et al.*, 2013), fertilization regimes (Edmeades, 2003), length of crop rotation (O'Rourke *et al.*, 2008; Rusch *et al.*, 2013) or the frequency and intensity of ploughing (Tamburini *et al.*, 2015, 2016).

Of all potential on-field management measures utilising ecological pathways for a sustainable agriculture, field-scale diversification has received the greatest attention – at least from the scientific community. Diversification practices counteract the recent trends of homogenizing agroecosystems on spatial and temporal scales, which has lowered the availability of resources and habitats for biodiversity (Benton *et al.*, 2003). Examples of diversification practices include mixed cropping, extended crop rotation schemes and the establishment of complex edge structures and flower plantings. Recent studies show that diversified cropping can enhance biodiversity and ecosystem services such as pollination and pest control (Kromp, 1999; Rusch *et al.*, 2010; Ratnadass *et al.*, 2012; Kennedy *et al.*, 2013; Dassou & Tixier, 2016; Tschumi *et al.*, 2016; Lichtenberg *et al.*, 2017; Boetzl *et al.*, 2018). Furthermore, and depending on the type of diversification practice, it may even promote win-win situations between conservation and productivity (Letourneau *et al.*, 2011; Pywell *et al.*, 2015; Gurr *et al.*, 2016; Tschumi *et al.*, 2016). However, this is not always the case if main crops are replaced with non-crops or cropping density increases in schemes with additive planting (Poveda *et al.*, 2008; Letourneau *et al.*, 2011; Iverson *et al.*, 2014). In the context of organic farming, extended crop rotations and mixed cropping reduce the often pronounced yield gap compared to conventional farming (Ponisio *et al.*, 2014), providing additional socioeconomic and environmental benefits.

I.2.2 Off-field pathways to ecological intensification

Similar to on-field homogenization (simple crop rotations, monocultures), landscape wide loss of habitat diversity and heterogeneity is a major cause of change in agroecosystems, directly or indirectly affecting insect and bird biodiversity and associated ecosystem services (Benton *et al.*, 2003). Management for ecological intensification and functional biodiversity comprises increases in heterogeneity of two landscape aspects: composition and configuration (Fahrig *et al.*, 2011). The effects of both aspects strongly depend on the study region, taxon and spatial scale considered (Gabriel *et al.*, 2010; Miguet *et al.*, 2013; Rusch *et al.*, 2013; Shackelford *et al.*, 2013; Jackson & Fahrig, 2015; Martin *et al.*, 2016). At the same time, composition and configuration variables are often strongly correlated, thus disentangling their individual and interactive effects is inevitable (Fahrig *et al.*, 2011).

Compositional aspects of heterogeneity include the amount of habitat within a landscape (e.g. natural or seminatural habitats, cropland, urban areas) or the overall assemblage of different habitat types (e.g. the diversity of habitats). Depending on the taxon and its required resources, low compositional heterogeneity often implies low functional diversity and abundance. This is particularly true for mobile species and the ecosystem services they provide. Pollinators, predators and birds are known to benefit from seminatural habitat and the availability of additional non-crop resources and habitats (Gardiner *et al.*, 2009; Fahrig *et al.*, 2011; Kirk *et al.*, 2011; Chaplin-Kramer & Kremen, 2012; Siriwardena *et al.*, 2012; Josefsson *et al.*, 2013; Gil-Tena *et al.*, 2015; Dainese *et al.*, 2016; Rusch *et al.*, 2016; Boesing *et al.*, 2017). Biological pest control can also respond positively to interannual changes in host plant cover (Schneider *et al.*, 2015; Bosem Baillod *et al.*, 2017).

A compositional aspect rarely considered is landscape-level crop diversity (i.e. the number and evenness of crops grown within a given landscape) (Fahrig *et al.*, 2011). Similar to non-crop aspects of landscape composition, crop diversity can enhance biodiversity and ecosystem services by providing complementary resources and habitats in space and time, facilitating the co-existence of species with multiple, seasonal extended resource requirements or different niches (Fahrig *et al.*, 2011; Kremen & Miles, 2012; Rusch *et al.*, 2013; Palmu *et al.*, 2014; Schellhorn *et al.*, 2015). The importance of crop resources may rise with increased homogeneity of non-crop habitats that are often deteriorated beyond functional importance (Martin *et al.*, 2016; Tscharntke *et al.*, 2016). Nevertheless, its role for biodiversity is ambiguous, showing very context-specific and opposing effects for insects (Palmu *et al.*, 2014; Fahrig *et al.*, 2015) and birds (Firbank *et al.*, 2008; Lindsay *et al.*, 2013; Fahrig *et al.*, 2015; Hiron *et al.*, 2015; Josefsson *et al.*, 2017). Even less clear is the function of crop diversity for ecosystem services such as biological pest control (Chaplin-Kramer & Kremen, 2012; Holland *et al.*, 2012; Bosem Baillod *et al.*, 2017). Nevertheless, it is now an integral part of the European Common Agricultural Policy, requiring farmers to reach specific levels of crop diversification ('Greening', EU Regulation No. 1307/2013). Similar to the enhancement of landscape-level hedgerow cover (Dainese *et al.*, 2016), this measure precludes yield losses due to cropland conversion or plant competition common to small-scale diversification practices (Lin, 2011). Concurrently, crop diversification enhances global food security and resilience against climate change by maintaining the functional redundancy of beneficial organisms (Lin, 2011; Bommarco *et al.*, 2013; Aguilar *et al.*, 2015; Schellhorn *et al.*, 2015).

Landscape configuration has received less attention than composition, despite evidence for its relevance as conservation measure and potential tool for ecological intensification. The spatial arrangement of habitats determines their connectivity and the dispersal ability of plants and animals, especially in strongly fragmented agricultural landscapes (Fahrig *et al.*, 2011). In heterogeneous landscapes, this often translates into benefits for ecosystem services. For instance, the distance to source habitats and the density of habitat patches affects wild bee richness and the pollination of wild plants (Hopfenmüller *et al.*, 2014; Ekroos *et al.*, 2015), although other taxa such as farmland birds may respond negatively to configurational heterogeneity (Hiron *et al.*, 2015). Nevertheless, recent studies highlight the value of small field sizes for both birds (Lindsay *et al.*, 2013; Fahrig *et al.*, 2015; Jeliazkov *et al.*, 2016; Josefsson *et al.*, 2017) and invertebrates (Kromp, 1999; Fahrig *et al.*, 2015; Bosem Baillod *et al.*, 2017). Similar advantages for the biodiversity of mobile predators have been found in landscapes with high edge density (large amount of ecotones, i.e. transition zones between habitats) (Martin *et al.*, 2016).

I.2.3 Interactive effects of on- and off-field variables

In many cases, management and landscape factors do not act in isolation, but interactively influence biodiversity, ecosystem services and yield (e.g. (Tamburini *et al.*, 2016; Bosem Baillod *et al.*, 2017; Gagic *et al.*, 2017)). For instance, the intermediate landscape complexity hypothesis states that management for biodiversity conservation is most effective in structurally simple rather than cleared out or complex landscapes (Tscharntke *et al.*, 2012). Similarly, landscape-scale crop diversity may be most relevant in landscapes with limited non-crop habitat (Palmu *et al.*, 2014; Josefsson *et al.*, 2017). Here, diversification or other extensification practices (i.e. lowering the intensity of farming) can provide additional habitats or essential resources otherwise lacking in the surrounding non-crop matrix (Tscharntke *et al.*, 2005; Josefsson *et al.*, 2017).

I.3 Liberating biodiversity

Disentangling the individual and interactive effects of on- and off-field practices for biodiversity and ecosystem services as well as their usefulness for ecological intensification is a major chore, especially in real-life ecosystems. Yet this was the main objective of the EU funded project Liberation (LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensification, http://www.fp7liberation.eu/home). The Europe-wide project (2013 – 2017) aimed to provide the evidence base for ecological intensification, and examined ecological, economic and social aspects of this approach (Figure I.2 B). It was novel in its assessment of synergies and trade-offs between different aboveground (pest control, pollination) and belowground (soil fertility, nitrogen mineralization) ecosystem services. For instance, a large joint experiment across the seven participating countries (Figure I.2 A) explored how local management practices (fertilizer application, insecticide input, field soil organic carbon) in combination with changes in cropland area at the expense of seminatural habitat determine the abundance of pests and predators, biological pest control, and crop yields in winter wheat (Gagic *et al.*, 2017). Additional analyses of existing datasets, modelling approaches and field or greenhouse studies examined, *inter alia*, general or interactive effects of management practices and landscape complexity on biodiversity, ecosystem service delivery and agronomic yield or income (e.g. (Marini *et al.*, 2015; Tamburini *et al.*, 2015; van Gils *et al.*, 2016). Although some of these studies used alternative cropping systems, the majority of research was conducted within cereal-dominated agroecosystems, with winter wheat being the main study crop.

The project Liberation was the setting of my doctoral thesis research, in which I investigated ecological pathways to ecological intensification in winter wheat, with a focus on 1) the relative effects of soil, management and landscape on biodiversity and yield in winter wheat (Chapter II), 2) the role of landscape-level crop diversity on biological pest control (Chapter III) and overall/functional bird diversity (Chapter IV), and 4) obstacles and opportunities for implementing ecological intensification (Chapter V).

I.3.1 Introducing the system

Winter wheat (*Triticum aestivum* L.) provides *c.* 19% of the global dietary energy, highlighting its vital role as staple food. Despite steady increases in global winter wheat productivity over the past decades, yields have stagnated or declined in 37% of winter wheat production areas, indicating limits to growth (Ray *et al.*, 2012). These limits are not necessarily set by factors that initially drove major productivity rises during the green revolution (crop breeding and the intensive use of agrochemical). Instead, they may be dictated by above mentioned on- and off-field factors (Chapter II) that are either out of practitioner's control (soil type, soil pH) or open for adjustment and adaption on farm or regional scales (crop management, landscape heterogeneity). These factors control some of the most limiting, scarcest resources in modern agricultural landscapes: biodiversity-mediated ecosystem services (application of Liebig's law of the minimum, first developed by Carl Sprengel in 1828).

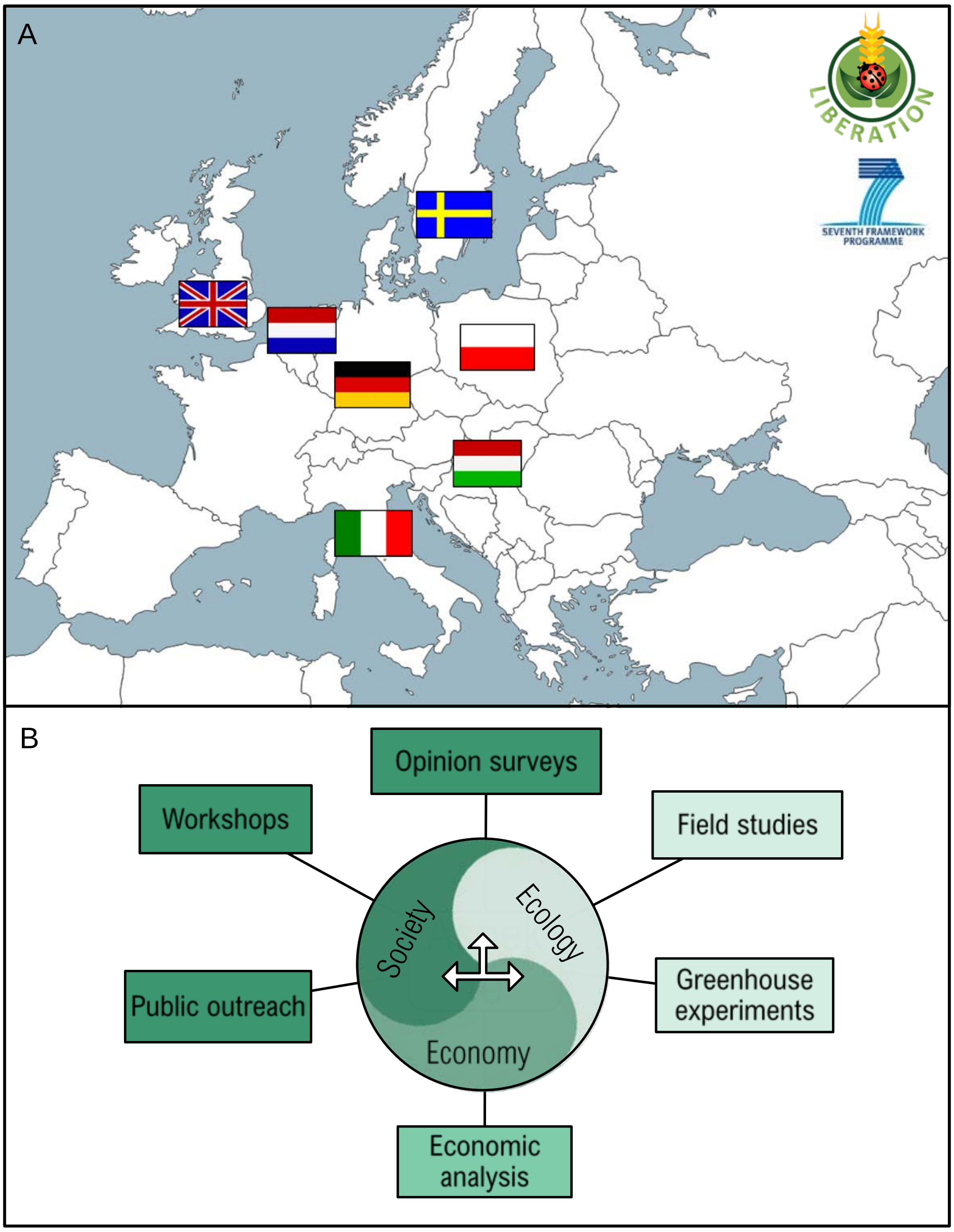


Figure I.2 Countries participating in the project Liberation (A) and methods used to explore ecological, social and economic aspects of ecological intensification (B).

Although winter wheat is wind pollinated and therefore does not depend on pollination by wild animals, this staple crop is highly susceptible to pests, with the total potential (without crop protection) and actual (with crop protection) losses to wheat yield estimated at around 50 and 28%, respectively (Oerke, 2006). Next to weeds and pathogenic fungi such as *Fusarium* spp., *Septoria* spp. and rust, winter wheat is highly susceptible to bird, rodent and arthropod pests, especially infestations and virus transmission by aphids (Hemiptera: Sternorrhyncha, most notably in Europe the cereal grain aphid *Sitobion avenae* (Fabricius)) and feeding damage by cereal leaf beetle larvae *Oulema* spp. (Figure I.3) (Oerke, 2006; Dedryver *et al.*, 2010). For winter wheat in Germany, the economic threshold of pest infestation has been estimated at 3 to 5 aphids per ear (milk ripening phase) and 0.5 to 1 *Oulema* eggs/larvae per leaf (Landwirtschaftskammer NRW, 2012).

Pests in winter wheat are regulated by a diverse array of natural enemies (Figure I.3) ranging from specialized biological control agents such as parasitoids (Hymenoptera, Parasitica) and ladybird larvae (Coleoptera: Coccinellidae) to generalist predators such as ground beetles (Coleoptera: Carabidae) and spiders (Araneae, various families) (Dedryver *et al.*, 2010). In the US, the value of insect-mediated pest control is estimated at US$13.6 billion (Losey & Vaughan, 2006). Biological control of *Sitobion avenae* in Southeast England alone may be worth up to US$ 3 Million. Therefore, losses in insect biodiversity and abundance observed over the last decades (75% in some areas of Germany (Hallmann *et al.*, 2017)) will inevitably translate into economic ramifications. While this insect ‘Armageddon’ (Dave Goulson, highlighting the ecological consequences of insect declines), has only recently attracted global public and political attention, negative trends in bird biodiversity are well documented and widely bemoaned.

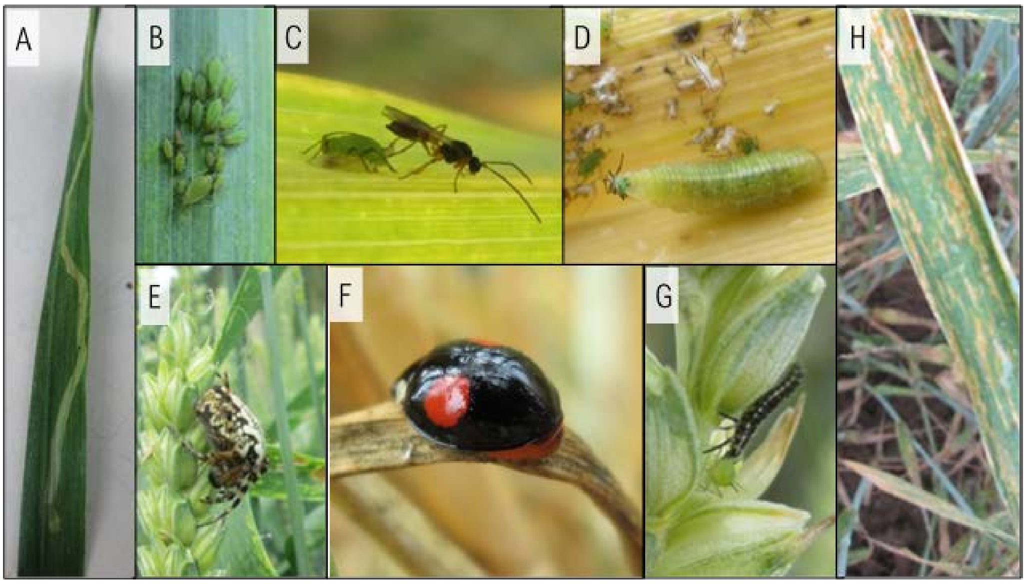


Figure I.3 Examples of protagonists (or their damage) associated with temperate winter wheat systems. Cereal leaf beetle *Oulema* larvae can cause serious feeding damage to leaf tissue (A). The most dominant and damaging pest is the cereal grain aphid *Sitobion avenae* (B) and regulated by a variety of parasitoids (C) and predators such as syrphid larvae (D), web-building spiders (E), ladybird adults (F) and larvae and hoverfly larvae (G). Weeds and pathogenic fungi such as rust (H) greatly influence wheat productivity. Pictures © Redlich

Birds are a charismatic taxon of great cultural and economic importance. Bird watchers and recreational hunters in the US spent over US$2 billion a year on a chance to encounter birds in their natural habitats (Pimentel, 2005). However, of the 1923 bird species listed as threatened or near-threatened on the global IUCN Red List, 37% and 45% of species, respectively, are endangered by intensive farming (Green *et al.*, 2005; Kirk *et al.*, 2011). This risk is greater for birds directly dependent on farmland habitat. 30 European farmland birds show significantly negative population trends (Gregory *et al.*, 2005; Voříšek *et al.*, 2010) and their overall abundance nearly halved over the last three decades (Gregory *et al.*, 2005; BirdLife International, 2018). Yet birds also occupy an important ecological niche. Some species actively contribute to biological pest control by feeding on herbivorous arthropods, thereby enhancing plant biomass and productivity in tropical and temperate crop and non-crop environments (Tremblay *et al.*, 2001; Puckett *et al.*, 2009; Mooney *et al.*, 2010; Maas *et al.*, 2013; Ndang'ang'a *et al.*, 2013b). On the other hand, they can constrain insect-mediated biological control via intraguild predation on intermediate predators (Mooney *et al.*, 2010; Mäntylä *et al.*, 2011; Martin *et al.*, 2013). These antagonistic species interactions (Straub *et al.*, 2008; Letourneau *et al.*, 2011) often counteract positive biodiversity-ecosystem service relationships (Altieri, 1999; Harrison *et al.*, 2014), emphasising the importance of not only assessing biodiversity effects, but also measure the actual ecosystem service provided by naturally-occurring assemblages of predators (Chapter III).

Insect and bird natural enemies vary in their importance for biological pest control (Schmidt *et al.*, 2003; Caballero-López *et al.*, 2012; Holland *et al.*, 2012; Martin *et al.*, 2013; Rusch *et al.*, 2013; Tamburini *et al.*, 2016; Dainese *et al.*, 2017). Furthermore, they respond to different management and landscape aspects across a range of spatial and temporal scales, depending on their mobility and resource dependence, and the study region or system (Gabriel *et al.*, 2010; Miguet *et al.*, 2013; Rusch *et al.*, 2013; Shackelford *et al.*, 2013; Jackson & Fahrig, 2015; Martin *et al.*, 2016). In fact, not all functional animal groups benefit from non-crop habitat and diversification, as exemplified for the bird taxon (Chapter IV). For instance, farmland birds, despite the generally detrimental influence of agricultural intensification on their diversity and abundance, are highly adapted to open, prairie-like landscapes associated with agroecosystems. It is therefore essential to investigate functional group responses to management and landscape factors that serve as potential tool of ecological intensification (Chapter II & IV), and study effects on overall ecosystem service provisioning (Chapter III). The winter wheat-pest-antagonist system provides ample opportunities to assess aspects of ecological intensification on different levels of the system, not only for one scale (Chapter II), but also using multiscale approaches (Chapter III & IV) that help to identify the optimal scale of landscape management. The high level of pesticides used and the strong responsiveness to agrochemical inputs and ecological processes suggests that opportunities for ecologically intensifying this system exist by compensating potential yield losses via the enhancement of ecosystem services such as biological pest control.

I.3.2 Introducing the overall research design

One major component of the project Liberation was a large-scale, joint field experiment assessing impacts of agrochemical use and landscape simplification on pest and natural enemy biodiversity, ecosystem services and yield (Gagic *et al.*, 2017; Garratt *et al.*, 2018b). For this purpose, a common field study was developed, with an average of 16 paired winter wheat fields in each participating country. My doctoral research, conducted in 2014 near Würzburg, Germany (49°47` N, 9°57` E), built upon this design by extending it to 28 fields in 14 landscapes, paired according to contrasting soil organic carbon content (Figure I.4, details in Chapter II). The study area has a long history of intensive agricultural management. Dominant agricultural crops are cereals, sugar beet, maize and oil crops that require high inputs of agrochemicals, especially fertilizer. At the same time, the region is still comparatively heterogeneous on larger scales due to forest remnants, calcareous grasslands and vineyards along the river Maine. This creates a mosaic of landscapes of various degrees of heterogeneity ranging from highly simplified (up to 95 % arable land) to more complex (around 15 % arable land). Landscapes were situated along this gradient of landscape heterogeneity, and, in addition, were selected to minimize correlations of compositional and configurational landscape aspects with landscape-level crop diversity at multiple spatial scales (100 to 3000 m radii around focal fields, Figure I.4). Depending on the study question, all or a subset of fields were used for my thesis research (Figure I.4).

The standard experimental design of the Liberation project was implemented on all study fields, with four subplots of 12 x 14 m size located on one of the field edges. A crossed insecticide-fertilizer treatment was applied haphazardly (Figure I.5 A & B, details see Chapter II). Pictures of fields were taken at every visit (Figure I.5 C – E) and plant growth monitored regularly (Figure I.5 F) to synchronize treatment application and experiments with collaborators.

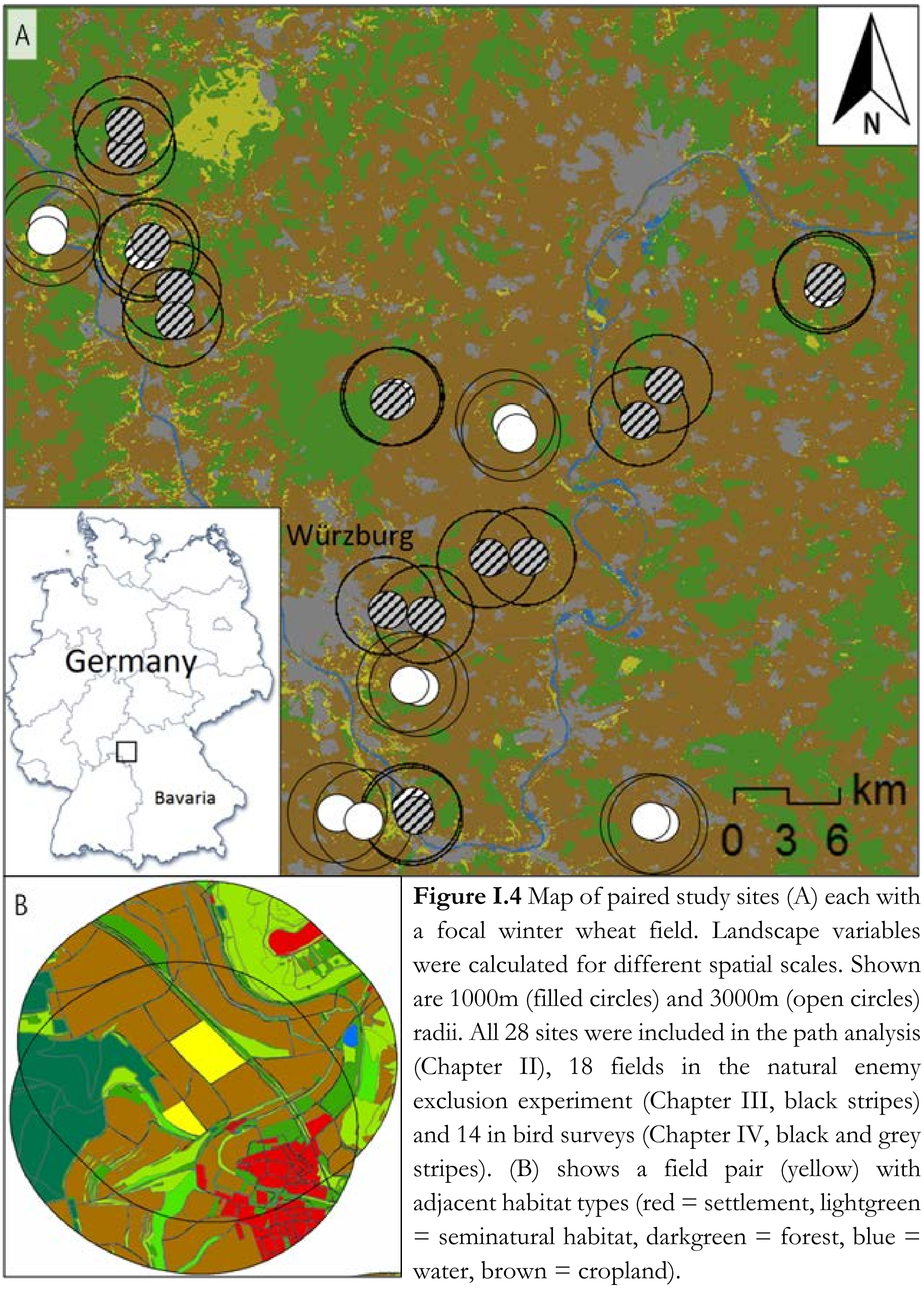


Figure I.4 Map of paired study sites (A) each with a focal winter wheat field. Landscape variables were calculated for different spatial scales. Shown are 1000m (filled circles) and 3000m (open circles) radii. All 28 sites were included in the path analysis (Chapter II), 18 fields in the natural enemy exclusion experiment (Chapter III, black stripes) and 14 in bird surveys (Chapter IV, black and grey stripes). (B) shows a field pair (yellow) with adjacent habitat types (red = settlement, lightgreen = seminatural habitat, darkgreen = forest, blue = water, brown = cropland).

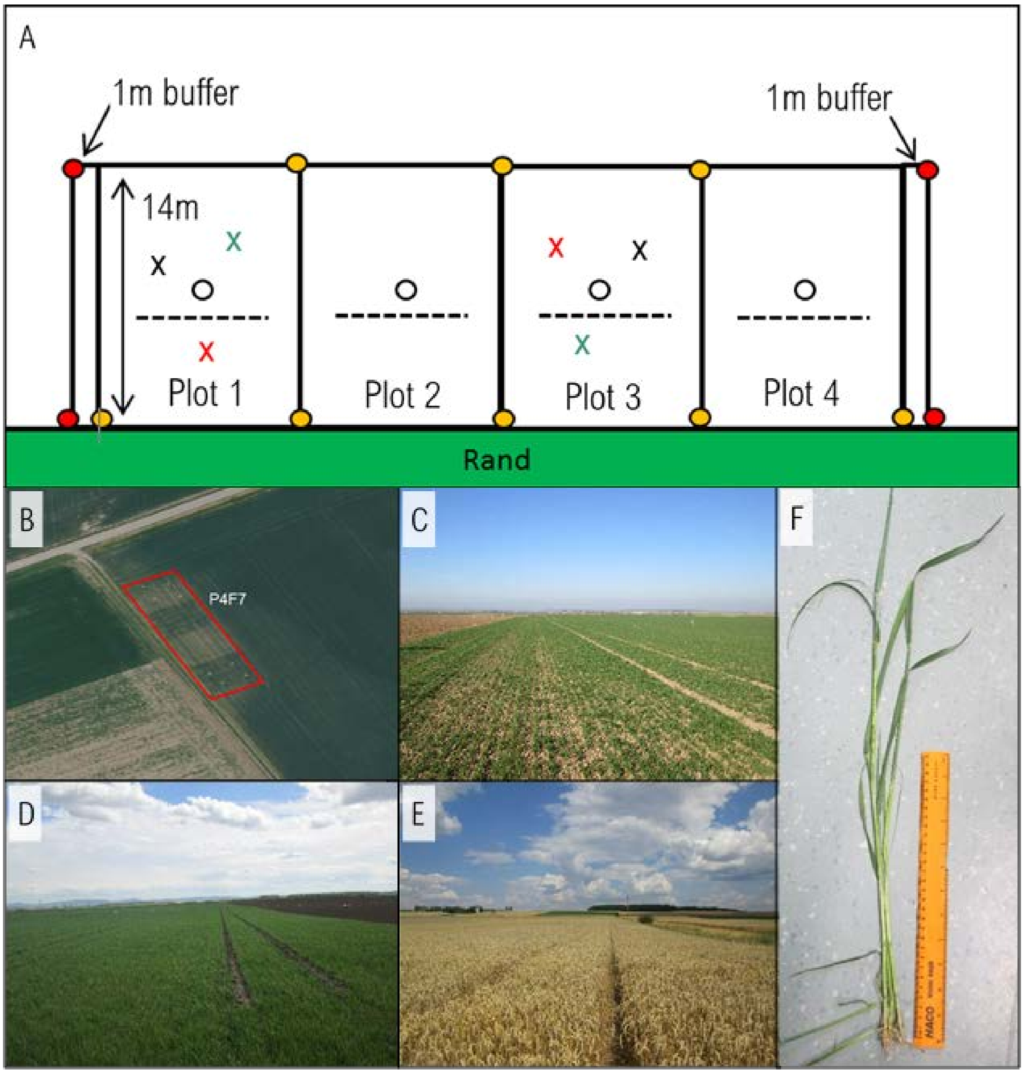


Figure I.5 Experimental set-up of study plots in 28 winter wheat fields (A). Four subplots were established on one of the open field edges. Fertilizer and insecticide treatments were applied randomly on subplot level (B, see Chapter II). Plant growth and development was documented with pictures (C-E, fields at establishment, midseason and at harvest, respectively) and assessment of the BBCH (F, plant growth stage). Within each subplot, transect surveys (dashed lines) and pitfall traps (circles) were used to assess the abundance and diversity of pests and natural enemies (A). Natural enemy exclusion cages (black cross = open control, red cross = full exclosure, green cross = bird exclosure) measured biological control potential in non-insecticide plots on 18 selected fields (see Chapter III). Pictures © Redlich

We conducted transect surveys and pitfall trap sampling on all 28 fields to assess the abundance and diversity of arthropod pests and natural enemies (Figure I.5 A). Data on weed pressure and infestations of winter wheat with pathogenic fungi was collected along the same transects. At the end of the growing season, samples of wheat were harvested from every subplot. This complete data set, coupled with detailed information on soil characteristics, present/historic crop management and landscape aspects was used to assess the relative effects of on- and off-field factors on biodiversity and yield in winter wheat (Chapter II). Effects of landscape-level crop diversity on biological pest control (Chapter III) were investigated by establishing a natural enemy exclusion experiment on nine field pairs (Figure I.6, details see Chapter III). Point counts along 14 fields assessed landscape-level crop diversity effects on bird biodiversity (Chapter IV). Full details of the experimental setup are available in Chapters II to IV, and in Gagic *et. al* 2017.

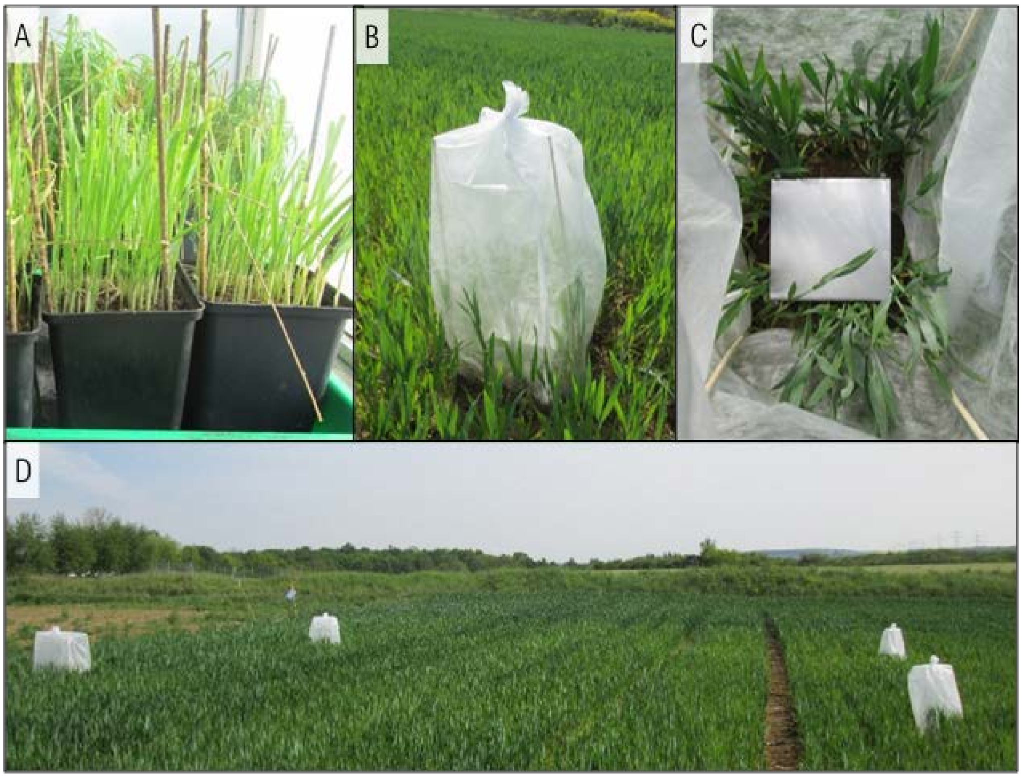


Figure I.6 Initial stages of the natural enemy exclusion experiment to assess effects of landscape-level crop diversity on biological pest control (Chapter III). Cereal grain aphids *Sitobion avenae* were reared on winter wheat (A), fiber tents (B) were erected and all pests and natural enemies within removed by hand and using pitfall traps (C) prior to aphid inoculation, with four tents within each non-insecticide plot (D). Ten days later, exclusion treatments were established (see Chapter III). Pictures © Redlich

I.4 Going the extra mile – from research to action

Disentangling the individual and interactive effects of on- and off-field soil, management and landscape aspects on biodiversity and ecosystem services helps to close the knowledge gap related to the mitigation of agricultural externalities. Although progress is comparatively slow, mostly due to the complexity of real-life ecosystems and potential synergies and trade-offs of mitigation methods, some important advances have been made in the field of ecological intensification. Unfortunately, research findings are rarely implemented, more commonly in social, health and conservation than in agricultural sciences (Ormerod *et al.*, 2002; Anonymous, 2007; Born *et al.*, 2009; Agre & Leshner, 2010; Memmott *et al.*, 2010; Eagleman, 2013; Hulme, 2014). This knowledge and implementation gap jeopardizes the utility of alternative farming approaches such as ecological intensification. Research can only promote change if it reaches the end users of knowledge: practitioners and policy makers.

Accordingly, an important component of the EU project Liberation was the dissemination of knowledge to stakeholders and the general public. Supported by my colleague Dr. Audrey St-Martin, I organized and conducted numerous outreach activities ranging from an information booth at the bi-annual agricultural exhibition of the German Agricultural Society in (DLG), talks (e.g. within the DLG forum during field exhibition, as invited speaker in the plant protection committee of the DLG or the seminar series of the biosphere reserve Rhön), a radio interview (SWR2 Impuls – Das Wissensmagazin), several press releases and, most importantly, two stakeholder workshops on a regional demonstration farm (Figure I.4). These dissemination activities were the foundation of TREE, a guideline aimed at enhancing the uptake of ecological intensification or other ecological farming approaches by emphasizing the crucial role of stakeholder engagement before, throughout and after implementing a research project (Chapter V).

Figure I.4 Impressions of the public outreach activities within the project Liberation. Information booth (A) and flower strip (B) at the DLG agricultural exhibition, public talk in the DLG forum (C), showcasing identification guides and nests of solitary bees (D) and sampling methods for pollinators and ground-dwelling arthropods (E), stakeholder workshop (F) and guided tour of demonstration farm (G) led by collaborating farmer Werner Kuhn (owner of demonstration farm). Pictures © Redlich & Wischemann

I.5 Thesis in a nutshell

This thesis is a compilation of research I conducted within the project Liberation, with the main aim of exploring the role of soil, management and landscape factors on biodiversity, ecosystem services and ecological intensification. It comprises four parts, covering different aspects of a cereal-pest-antagonist system, and highlighting the contribution of stakeholder engagement in the transfer from research to action.

Biodiversity and yield can be influenced by a variety of on- and off-field factors, and assessing their relative importance is an essential first step towards identifying alternative pathways to ecological intensification. Therefore, I used the combined set of 28 winter wheat fields to investigate the role of 34 soil, crop management (recent and historic) and landscape variables for arthropod pests, natural enemies and yield components. For this purpose, I crossed an observational study of biodiversity in real-life agroecosystems with an on-field insecticide-fertilizer experiment. This is one of the first studies to concurrently quantify the effects of numerous drivers usually studied in isolation. (Chapter II).

Landscape effects on biodiversity vary depending on the spatial scale considered, so that choosing an inappropriate scale could mask existing beneficial effects. Simultaneously, positive relationship between landscape heterogeneity and natural enemy diversity and abundance does not always translate into enhanced biological pest control, as intraguild predation may interfere. This is particularly true for trophic interactions related to birds and their arthropod (predatory) prey. Using a natural enemy exclusion experiment, I assessed the influence of multi-scale landscape-level crop diversity on biological pest control of the cereal aphid *Sitobion avenae* on 18 winter wheat fields. The role of avian predation for total and insect-mediated biological control was examined with the selective exclusion of insectivorous birds (Chapter III).

Responses to landscape aspects such as crop diversity strongly depend on the taxon and functional group considered, as resource and niche requirements vary. For example, farmland, insectivorous or red-listed birds may show diverging relationships with crop diversification, both in relation to its importance and the scale of effect. These diverging responses between functional groups (feeding guild, conservation status, habitat preference, nesting behaviour) were assessed in an observational study of bird biodiversity on 14 winter wheat fields (Chapter IV).

Identifying ecological pathways that favour biodiversity and ecosystem services provides tools for ecological intensification that increase the likelihood of balancing conservation and productivity goals. However, change will be slow to come if research findings are not implemented on a global scale. In my last paper, I develop the 'TREE' concept (Target-Research-Engage-Exploit), which builds upon feedback and stakeholder opinions collected in numerous dissemination activities. TREE acts as a guide for scientists aiming to increase the applied impact of their research and facilitate the uptake of ecological intensification. (Chapter V).

Chapter II

Ecological pathways to high yields in conventional cereal systems

Conventional farming is associated with large-scale threats to biodiversity, the disruption of ecosystem services and long-term risks for food security and human health. Here, we use a real-life ecosystem approach to explore ecological pathways to high yields in German cereal systems, whereby enhanced natural pest control allows for the reduction of intensive agricultural practices. On 28 conventional winter wheat fields selected along a gradient in landscape heterogeneity, we conducted field experiments with crossed insecticide-fertilizer treatments. We then used path analysis to assess the direct and indirect effects of pesticide use, landscape heterogeneity, soil characteristics, weed and disease pressure, historic and current field management, pest and natural enemy abundances on yield. We identify a range of soil and management characteristics that enhanced productivity independently of external agrochemical inputs (e.g. reduced soil preparation, high crop rotation diversity). Simultaneously, pest control potential could be restored by strengthening observed links between natural enemies and landscape heterogeneity (mean field size) or local management aspects (crop rotation diversity, no-till). We conclude that wheat systems offer a range of ecological pathways by which ecosystem services could be enhanced while reducing agrochemical usage and negative environmental impacts of conventional agriculture.

II.1 Introduction

Functional biodiversity generates essential ecosystem services to agriculture such as biological pest control, pollination and soil services (e.g. nutrient cycling). Yet intensive agricultural practices cause large-scale threats to biodiversity, and consequently they disrupt ecosystem services and pose long-term risks for food security and human health. A potential solution is offered by the ecological intensification of farming, which aims to manage yield-supporting ecosystem services to minimize external inputs and enhance agricultural sustainability (Bommarco *et al.*, 2013; Pywell *et al.*, 2015; Gurr *et al.*, 2016). For ecological intensification to be effective, it is essential to identify ecological pathways able to sustain yields while using less intensive conventional farming practices.

Winter wheat (*Triticum aestivum* L.) is one of the most important staple foods in the world, providing *c.* 19% of global dietary energy. Although global wheat productivity has increased steadily over the last decades, 37% of production areas show stagnating yields, indicating limits to growth (Ray *et al.*, 2012). These limits are set by a variety of on- and off-field factors: soil characteristics including soil organic matter content (Tamburini *et al.*, 2015; Gagic *et al.*, 2017), crop management (e.g. sowing density, fertilization regime (Edmeades, 2003; Ozturk *et al.*, 2006; Valério *et al.*, 2013)), and natural processes such as herbivory, infections with pathogenic fungi and pest control (Dedryver *et al.*, 2010). Additional indirect effects on yield are mediated by the consequences of soil conditions (Birkhofer *et al.*, 2008; Kremen & Miles, 2012), agricultural management (von Berg *et al.*, 2010; Garratt *et al.*, 2011; Krauss *et al.*, 2011; Jonsson *et al.*, 2012; Tamburini *et al.*, 2016) and landscape heterogeneity (Fahrig *et al.*, 2015; Martin *et al.*, 2016; Bosem Baillod *et al.*, 2017; Redlich *et al.*, 2018) on pest-enemy interactions and soil services (e.g. nutrient cycling). Further, these soil, management and landscape factors often do not act in isolation, but may interactively influence predators, prey, and yield (e.g. (Tamburini *et al.*, 2016; Bosem Baillod *et al.*, 2017; Gagic *et al.*, 2017)). To date, it is still unclear how multiple factors influence yields, and which ecosystem services could be utilized for ecological intensification by replacing or reducing current external inputs. Furthermore, not all potential direct or indirect drivers of wheat productivity lend themselves to manipulation. Yet, these need to be acknowledged in order to assess the relative importance of alternative pathways for yield provision.

In this study, we aim to identify ecological pathways able to maintain high yields in conventional wheat systems by utilizing biological pest control services. Within a landscape heterogeneity gradient, we implemented a factorial on-field pesticide experiment and quantified potential drivers of yield related to five broad categories (Figure II.1), based on agro-ecological theory. We deliberately chose a real-life exploratory approach to account for criticism by practitioners regarding the transferability of results from small-scale, controlled experiments to real agroecosystems. In real-life systems, interactions among management or landscape factors commonly result in unexpected outcomes (Tylianakis *et al.*, 2008), thereby curtailing anticipated benefits for farmers and their trust in the practical applicability of research. We thus specifically included factors usually studied in isolation (e.g. pathogen occurrence, soil characteristics and historic crop management). We used structural equation modelling (SEM) to disentangle direct and indirect linkages between drivers and yield components (Figure II.1). We expected that 1) local crop management, soil characteristics and landscape heterogeneity determine pest pressure (including weeds and diseases) and the abundance of natural enemies; 2) relationships between trophic levels (crop-pests-predators) can be either negative (top-down processes, i.e. herbivory and pest control) or positive (resource-driven, bottom-up processes, i.e. host and prey availability)(Vidal & Murphy, 2018); and 3) combined effects of agrochemical inputs, soil services and pest control determine realised yields. .

II.2 Materials and Methods

II.2.1 Study design

Study design followed a paired-field design described in (Gagic *et al.*, 2017) (Appendix 1, Figure II.S1). Fourteen pairs of winter wheat fields (28 fields) were selected in 2014 near Würzburg/Germany (49°47` N, 9°57` E) along a landscape heterogeneity gradient defined by the % seminatural habitat cover within a 1 km radius around fields. Fields were paired according to contrasting soil organic carbon content (SOC). Average distance (mean±SD) within and between field pairs was 1.07±0.9km and 11.21±3.75km. On each field, a randomized, fully-crossed experiment with pyrethroid insecticide (yes/no) and mineral fertilizer application (yes/no) was implemented in four treatment plots (12x14m each) (Appendix 1).

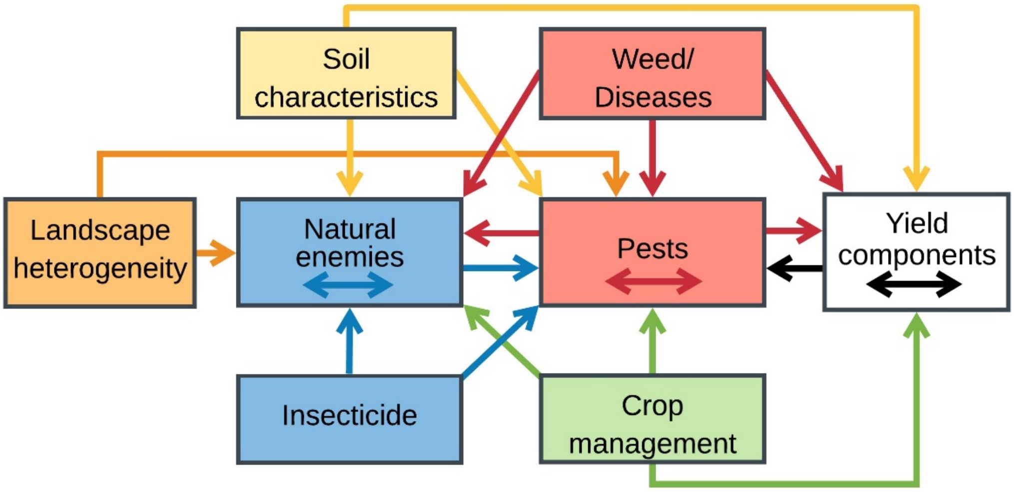


Figure II.1 Conceptual diagram used for path analysis, showing expected direct and indirect effects of ecosystem services on yield components (grain yield, thousand kernel weight, plant biomass; white). Drivers of productivity may relate to pest regulation (approximated by natural enemy abundances, insecticide application; blue), pests and diseases (pest abundances, weed cover, incidence of pathogenic fungi; red), landscape heterogeneity (aspects of landscape composition and configuration such as mean field size; orange), soil characteristics (soil type, pH, organic matter content; yellow) and current and historic crop management (e.g. sowing density, fertilization, crop rotation diversity; green). Arrows indicate the expected direction of the effect. Double-ended arrows show potential species interactions within groups.

II.2.2 Direct and indirect drivers of yield

A total of 34 explanatory variables were considered as direct or indirect drivers of yield in our system. A first set of environmental variables related to soil characteristics and SOC content as a proxy for SOM. Crop management data was derived from the experimental set-up (fertilizer application) and from farmer surveys performed in autumn 2014. Farmer surveys covered past (mean data availability 11.25 ± 0.43 years) and recent crop management information. Landscape heterogeneity was assessed in circular areas of 1 km radius around study fields using ArcGIS v. 10.4 (ESRI) with a focus on variables relevant for pests and arthropod antagonists, including variables of landscape configuration and composition (see Supplement, Table II.S2).

A second set of biotic variables included the abundance and activity density of pests and natural enemies in treatment plots (*n*=112). For this we considered eight functional groups of pests and natural enemies. Leaf-dwelling predators and pests were assessed in three consecutive visual transect counts (one before, two after insecticide application), then summed to estimate pest pressure and pest control potential throughout the growing season (Appendix 1). Due to differences in the feeding behaviour of aphids (Hemiptera: Sternorrhyncha), we distinguished between the English grain aphid *Sitobion avenae* (Fabricius) which preferentially feeds on the grain, and the rose-grain aphid *Metopolophium dirhodum* (Walker) which feeds on stem and leaves. Cereal leaf beetles *Oulema* spp. (Coleoptera: Chrysomelidae) were grouped as either larvae (sessile) or adults (winged). Leaf-dwelling predators were classed as 'active flyers' (ladybirds [Coccinellidae, adults and larvae], hoverflies [Syrphidae, larvae], lacewings [Chrysopidae, larvae]) or 'passive flyers' (wind-dispersed web-building spiders [Araneae]). Activity density of two groups of soil-dwelling predators (ground beetles [Carabidae] and ground-hunting spiders [mainly Lycosidae]) was determined using pitfall traps within each treatment plot for ten consecutive days (one sampling round after insecticide application). Additionally, we surveyed forb and grass weed cover in each treatment plot. As grass cover was low, only forbs were used in analyses. Incidence of the pathogenic fungi *Fusarium* and rust (*Puccinia* spp.) was assessed in two visual pathogen surveys (Appendix 1). These biotic variables covered the potential drivers related to pest or disease occurrence and pest regulation, the latter also including the experimental treatment 'insecticide application' (Figure II.1).

Details of variable measurement, sampling and summary statistics per plot are provided as supplementary material (Supplement, Table II.S1).

II.2.3 Estimation of yield components

In every treatment plot (*n*=112), we measured three aspects of yield, namely moisture-adjusted grain dry weight ('grain yield', t ha^{-1}), thousand kernel weight (TKW, g) and air-dried plant biomass (without grain, kg m^{-2}). These three yield components were treated as final response variables in our analysis (Supplement, Table II.S1).

II.2.4 Statistical analysis

To quantify direct and indirect effects of explanatory variables on yield components we developed a piecewise structural equation model (SEM) (Figure II.1). The SEM consisted of eleven individual path models with the response variables grain yield, plant biomass, TKW, *S. avenae*, *M. dirhodum*, *Oulema* larvae, *Oulema* adults, ground spiders, predatory carabids, active and passive flyers. Abundances of pests and predators were log-transformed to improve normality of residuals. A random intercept of Field nested in Pair accounted for multiple sampling within landscapes and fields. The linkages of individual path models were defined by performing linear mixed effects models of the responses against hypothesized, preselected predictors, with preselection based on ecological theory and Pearson's correlation values (Table II.S2). The SEM was then simplified by removing non-significant terms (p-values > 0.05) from resultant full individual path models using backwards elimination (Tables II.S2 & II.S3). Fixed terms with marginal p-values (0.05 – 0.1) or initially excluded from models for lack of known ecological theory only entered individual models if their inclusion increased SEM fit (based on AICc, mean field size influencing *S. avenae* abundance) or the directed separation test (D separation test (Shipley, 2009) revealed missing links with significant path coefficients (effects of sowing date on *M. dirhodum* and predatory carabids), respectively. As preliminary analyses did not reveal any interactive effects of soil characteristics and fertilisation regime on yield and soil-dwelling predators (Table II.S4), no interactions were included in individual path models. If partial correlation plots suggested non-linear relationships between response and explanatory variables, polynomial terms (quadratic or cubic) were fitted. For trophic relationships, we first assumed top-down, negative effects of enemies on pests and of pest variables on yield. However, if positive, resource-driven correlations were observed, the direction of links was adapted accordingly (Table II.S2). Final individual path models (Table II.S3) were validated graphically for normality, homoscedasticity and spatial auto-correlation (Moran's *I*, p-values >0.802). Collinearity in models was low (variance inflation factor <3).

The final, simplified SEM showed a good fit (D separation test, Fisher's C = 356.2, $P = 0.215$ (Shipley, 2009)). Conditional model fit (R^2) of individual path models was high, ranging from 37 to 74% of variance explained (Figure II.2). The relative importance of predictors included in the final SEM was assessed using standardised path coefficients scaled by mean and variance (Schielzeth, 2010).

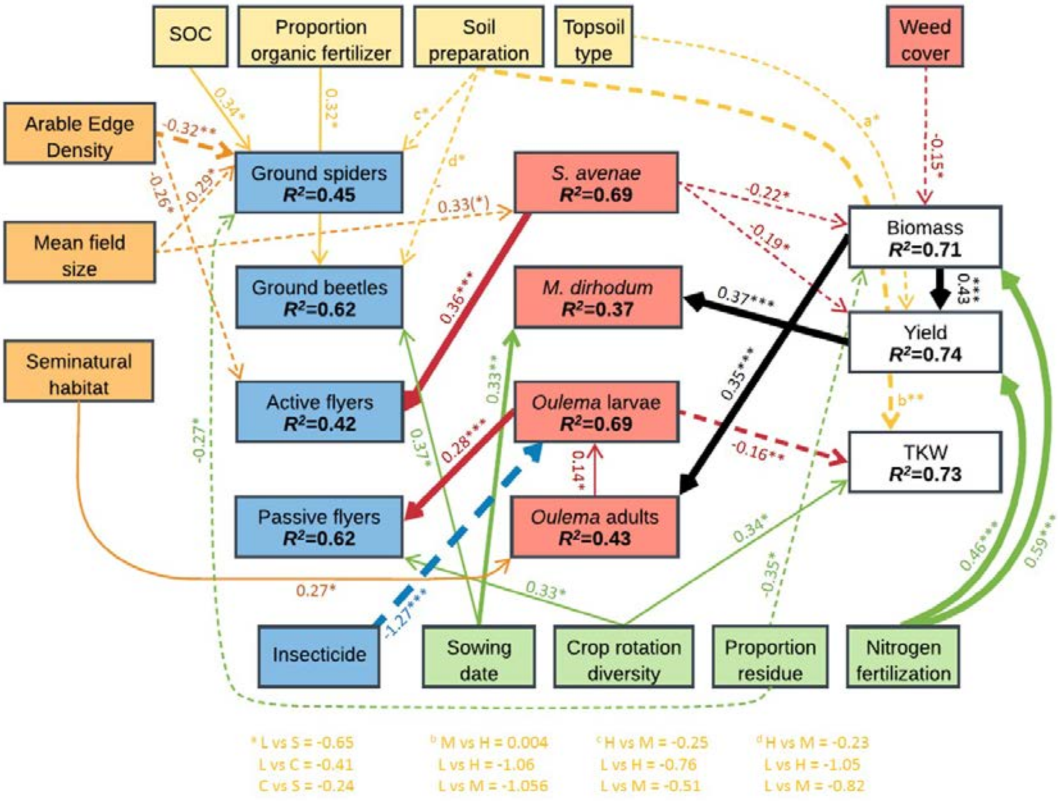
We used additional mixed effects models to assess whether responses to insecticide were masked by pooling abundance data across surveys. We fitted separate models for all pests and leaf-dwelling predators (no temporal sampling for soil-dwellers). Fixed terms were 'Survey' (three levels), insecticide application (yes/no) and their interaction. Post hoc Tukey multiple comparisons evaluated significant differences in abundance between surveys. A random term (Pair/Field/Plot) accounted for repeated sampling within each treatment plot.

All analyses were performed in R version 3.3.2 (R Development Team, 2016) using packages 'nlme'(Pinheiro *et al.*, 2016), 'PiecewiseSEM' (Lefcheck, 2016), 'car'(Fox & Weisberg, 2011) and 'visreg'(Breheny & Burchett, 2017).

II.3 Results

Our results reveal the combined direct effects of local management, insect pests, weeds and soil processes, and indirect effects of mainly natural enemy-mediated landscape factors on yield components. Grain yield, plant biomass and TKW per plot varied between 2.8 and 14.7 t ha^{-1} (mean±SE: 7.6±0.24), 0.2 to 1.7 kg m^{-2} (0.8±0.03) and 36.7 to 53.3 g (44.03±0.32), respectively. Differences in yield were directly related to soil characteristics, crop management and pest pressure, and to a range of indirect effects via trophic interactions (Figure II.2). Of the 18143 pests recorded, *Sitobion avenae* was the most abundant species (89% of individuals), followed by *Oulema* larvae (5%), *Metopolophium dirhodum* (4%), and *Oulema* adults

(2%). Pest abundances were largely management and resource-driven (Figure II.2). Similarly, predators (2594 in total) responded to prey abundances, yet were also influenced by crop management practices and soil characteristics (Figure II.2). The predator community sampled with visual surveys and pitfall traps was dominated by web-building spiders (48%) and predatory carabids (30%), whereas ground-hunting spiders (14%) and active flyers (8%, primarily Coccinellidae and Syrphidae) were least abundant.



ᵃ L vs S = -0.65
L vs C = -0.41
C vs S = -0.24

ᵇ M vs H = 0.004
L vs H = -1.06
L vs M = -1.056

ᶜ H vs M = -0.25
L vs H = -0.76
L vs M = -0.51

ᵈ H vs M = -0.23
L vs H = -1.05
L vs M = -0.82

Figure II.2 Path diagram of final SEM. Shown are direction (arrow), sign (negative = dashed line, positive = solid line), and strength (thickness of lines) of relationships between landscape heterogeneity (orange), soil characteristics (yellow), crop management (green), natural enemies (blue), pests and diseases (red) and yield components (white). The relative amount of explained variance (R^2) of individual path models, standardized path coefficients and their statistical significance ((*)$P<0.1$, *$P<0.05$, **$P<0.01$, ***$P<0.001$)) are given. Letters and footnotes indicate effects and coefficients of the three-level factors soil type (L = loam, S = sandy, C = clay) and intensity of soil preparation (L = low, M = medium, H = high).

II.3.1 Effects on yield

The yield components plant biomass and grain yield were strongly correlated (Figure II.2), and were both enhanced by fertilizer application (26% and 30% increase, respectively, Figure II.3 A+D). Grain yield (but not plant biomass) was significantly lower on soils with a high sand content (-36%, Figure II.3 B+E). However, weed cover and the frequency of residue left-over reduced plant biomass and indirectly grain yield (indirect effect via biomass, product of standardized path coefficient = -0.15 and -0.06). TKW was larger on fields with a high crop rotation diversity or no-till soil management (Figure II.S2 B+C). *S. avenae* had the strongest herbivory effect on yield quantity, reducing grain yield and plant biomass, with the negative slope being steeper for biomass (Figure II.3 C + F). In contrast, high population densities of *Oulema* larvae resulted in lower TKW (i.e. yield quality, Figure II.S2 A). Although the plant pathogens *Fusarium* and rust had no effect on yield, weed cover directly (plant biomasss) and indirectly (only indirect effect on grain yield via biomass -0.06) influenced yield (Figure II.2). Additionally, yield components were indirectly influenced by responses of pests to landscape and management variables.

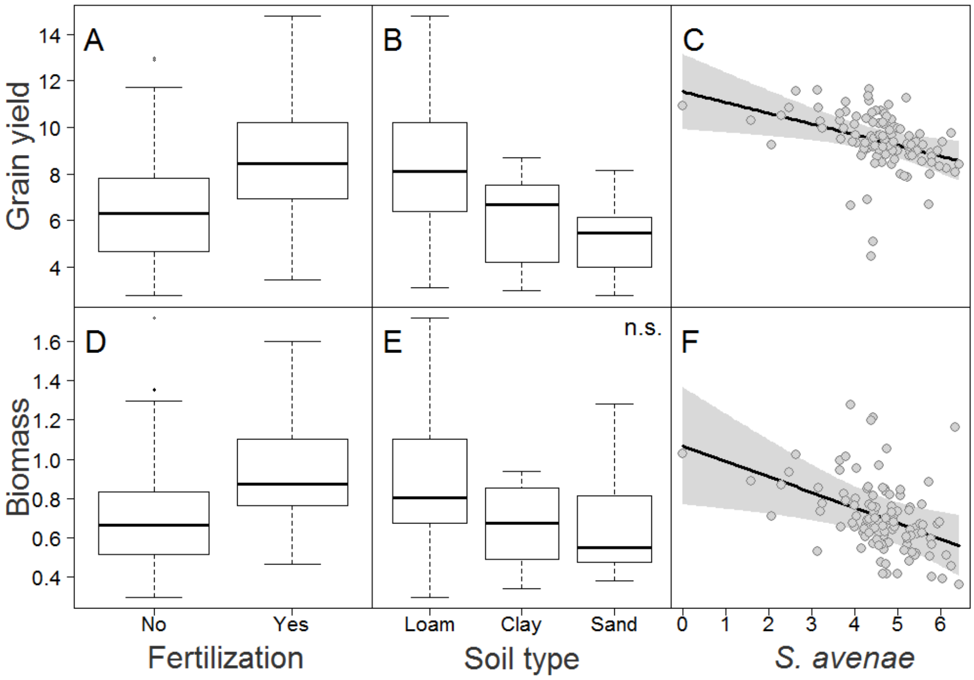


Figure II.3 Main direct drivers of yield. Effects of fertilization, soil type and abundance of *Sitobion avenae* (log-transformed) on grain yield (t ha^{-1}, A-C) and plant biomass (kg m^{-2}, D-F). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown. 'n.s.' non-significant relationship.

II.3.2 Effects on pests

The main direct drivers of pest abundances were related to resource availability. *M. dirhodum* and *Oulema* adults occurred in greater densities in plots with high grain yield or large plant biomass, respectively (Figure II.S3 B + C). Indirectly, both pests were therefore enhanced by nitrogen fertilization (indirect effects 0.17 and 0.2, respectively; Figure II.2). Moreover, *Oulema* adults (and indirectly offspring) were more common in landscapes with large seminatural habitat cover (Figure II.S3 F + G). In contrast, insecticide application decreased *Oulema* larvae abundances by 78% (Figure II.S3 D), which led to increased TKW (indirect effect 0.2). No other pest showed a similar response to insecticide in models with accumulated abundances used in the SEM. However, additional analyses using separate survey rounds showed 60% less *S. avenae* in plots sprayed with pyrethroid before the second survey, although aphid abundances recovered quickly (Tukey test insecticide vs. no insecticide, Survey 1: $P = 0.22$, Survey 2: $P < 0.001$, Survey 3: $P = 0.822$; Figure II.S4 A). For *Oulema* larvae, this effect was longer-lasting (Survey 1: $P = 0.99$, Survey 2: $P < 0.001$, Survey 3: $P = 0.026$; Figure II.S4 B). Along with short-term insecticide effects, *S. avenae* abundance was negatively correlated with mean field size in the landscape (Figure II.S3 A). Consequently, mean field size indirectly influenced grain yield and plant biomass (indirect effects 0.06 and 0.07, respectively; Figure II.2). Lastly, *M. dirhodum* showed positive responses to sowing date, with aphids being more abundant in fields sown later in the year (Figure II.S3 E).

II.3.3 Effects on natural enemies

Both groups of soil-dwelling predators strongly responded to reduced soil disturbance, i.e. no-till as opposed to deep ploughing (Figure II.4 A+D). Furthermore, predatory carabids had higher activity densities on fields with frequent organic fertilizer application and late sowing of winter wheat (Figure II.4 E, Figure II.S5 F). Densities of ground-hunting spiders increased with SOC content, yet declined with residue addition (Figure II.4 B, Figure II.S5 E). Leaf-dwelling predators were not affected by soil management, but wind-dispersed spiders were enhanced on fields with diverse crop rotations (Figure II.4 F). In contrast to soil-dwellers, both groups of leaf-dwellers also showed strong positive responses to prey density, in particular abundances of *S. avenae* (active flyers) and

Oulema larvae (passive flyers; Figure II.S5 B + C). Insecticide application indirectly affected wind-dispersed spiders by reducing *Oulema* larvae abundances (indirect effect = -0.36), yet we did not observe direct effects of insecticide on leaf-dwelling predators in our SEM analysis using accumulated abundances, nor in additional analyses using distinct survey rounds. Temporal effects of insecticide application could not be tested on soil-dwellers, as pitfall traps were only opened once after insecticide application (see Methods). Landscape variables were negatively related to predators, in particular ground-hunting spiders. Their activity density was lowest in landscapes with large fields and high arable edge density (Figure II.4 C, Figure II.S5 D).

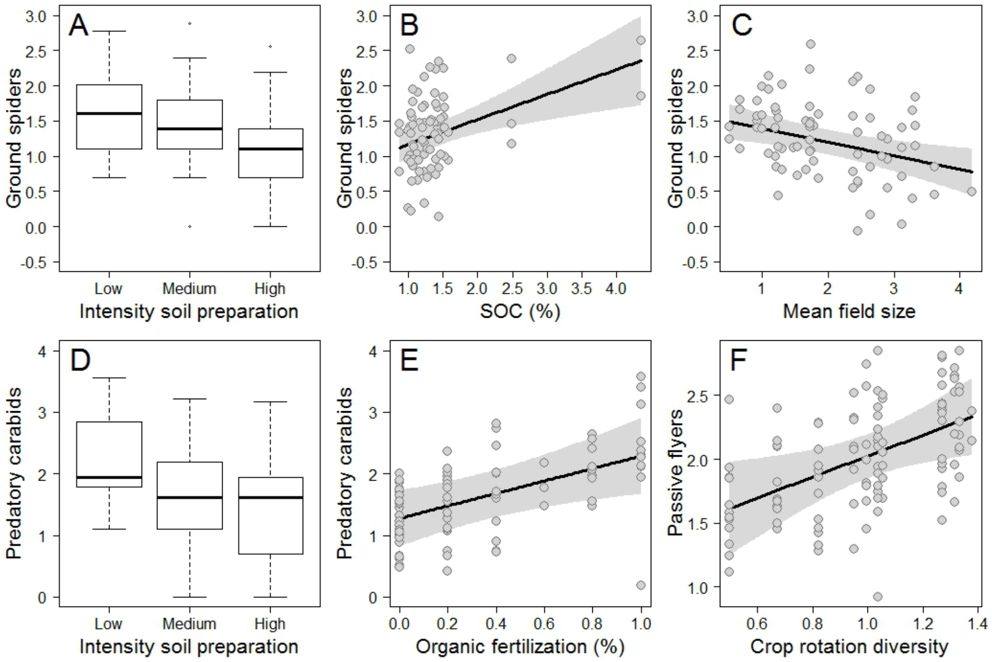


Figure II.4 Direct effects of management and soil variables on natural enemies (log-transformed). Relationships between activity density of soil-dwelling predators and soil preparation intensity (‘Low’ = no-till, ‘Medium’ = surface cultivation, ‘High’ = deep ploughing, A + D), soil organic carbon content (‘SOC’, B), mean field size (ha, C) and frequency of organic fertilization (E). Influence of crop rotation diversity on wind-dispersed spiders (F). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown.

II.4 Discussion

Growing food demand accompanied by ongoing health and environmental pressures call for more sustainable farming systems able to maintain current levels of productivity. Ecological intensification (i.e. utilizing ecosystem services) is a promising tool to achieve this goal. In this study, we investigated current multifactorial drivers of yield components in a real-life cereal agroecosystem, and reveal potential pathways for ecological intensification as alternative to external input-driven crop production.

Ambiguous effects of fertilizer and insecticide highlight alternative options for maintaining yield quality and quantity under conditions of reduced agrochemical inputs and extensified management. Even though grain yield and biomass were reduced in non-fertilized plots, so was pest pressure by *M. dirhodum* and *Oulema* larvae. Consequently, TKW, an important indicator for seeding vigour and milling quality of wheat, increased (Botwright *et al.*, 2002). While insecticides decreased *Oulema* larvae, *S. avenae*, the most abundant and yield-damaging pest, was not effectively controlled, as its numbers quickly rebounded after short-term insecticide-driven reductions, as has been found elsewhere (Krauss *et al.*, 2011). Negative effects of insecticide on relatively mobile leaf-dwelling predators were not found, possibly due to rapid resettlement after spraying. Pitfall traps were established after insecticide application, so we were unable to assess whether soil-dwelling spiders and predatory carabids were more abundant before insecticides were sprayed.

Yet our results highlight additional ecological pathways to higher yield, primarily by enhancing soil-dwelling predators via local soil and crop management. High soil organic matter content favours saprophagous insects such as springtails that are important alternative prey for soil-dwellers early in the year, and allow for the build-up of large predator populations. However, ploughing alters physical characteristics of the soil and speeds decomposition of soil organic matter (Tilman *et al.*, 2002), causing unfavourable conditions for below-ground prey. Soil-dwelling predators and associated pest control (Tamburini *et al.*, 2015, 2016) therefore benefit from the combined effects of soil conservation practices (no-till, high SOC). High initial densities of soil-dwelling predators at the beginning of the growing season are imperative for reducing initial pest infestations, but top-down control by this predator group may be lower or non-significant later on, as observed here (Barrios, 2007; Birkhofer *et al.*, 2008). Predators such as wind-dispersed spiders may also rely on increased temporal resource diversity and reduced chemical inputs inherent to diverse crop rotations (McLaughlin & Mineau, 1995). Moreover the enhanced condition and nutritional balance of diversely cropped, no-till soils also provides optimal growing conditions for a high quality crop (McLaughlin & Mineau, 1995; Ratnadass *et al.*, 2012), as shown here by enhanced TKW. In addition, timely (as opposed to late) sowing of wheat allows for earlier crop maturation and can reduce pest pressure (Acreman & Dixon, 1985), as seen for *M. dirhodum.* While we observed a similar effect on predatory carabids, this response was less pronounced.

In contrast to soil and crop management, the role of landscape heterogeneity was low in our system. Although 1000m radius is commonly used in ecological studies of pest control (e.g. (Rusch *et al.*, 2013; Tamburini *et al.*, 2016; Bosem Baillod *et al.*, 2017)), the spatial scale of heterogeneity effects differs depending on the life history and movement capability of taxa (Chaplin-Kramer *et al.*, 2011; Martin *et al.*, 2016; Redlich *et al.*, 2018). Here, we observed opposing relationships between measures of configurational heterogeneity and ground-hunting spiders, with spiders responding positively to small field sizes, but not to increased edge density. Predators in landscapes with small fields benefit from easy access to field boundary habitat and on-field prey (Fahrig *et al.*, 2015), yet a high density of crop-non crop borders may hinder their dispersal into fields if their structure acts as barrier or provides competing resources (Ratnadass *et al.*, 2012). Opposed to previous studies, we did not observe reduced pest densities with increased landscape heterogeneity (Bianchi *et al.*, 2006; Bosem Baillod *et al.*, 2017) or host crop cover (Schneider *et al.*, 2015), but more *Oulema* and *S. avenae* in landscape with high amounts of seminatural habitat and smaller fields. Additional habitats and easy access to fields may favour these pests. Alternatively, these landscape may experience lower, landscape-wide spraying intensities, a possible correlation we did not measure.

Lastly, we observed no effects of some factors often considered important, or found differences in the responses of yield components. This may be due to the ability of wheat to compensate for unfavourable soil conditions, weed competition and crop damage caused by pathogenic fungi or herbivory via changes to other yield components (e.g. tiller density, number of grains per spike) (Freeze & Bacon 1990). For instance, crop damage by the plant pathogens rust and *Fusarium* (maximum infestation rate 58% and 34%, respectively), and feeding damage by *Oulema* larvae were very obvious on some fields, yet with the exception of TKW, our data did not confirm fears of participating farmers that this would lead to important yield losses. In addition, yield reductions due to weed cover and *S. avenae* infestation had a greater negative effect on plant biomass than on grain yield, indicating that at the levels reached in our system, controlling these factors by agrochemical means is less critical than expected for final crop productivity.

II.5 Conclusion

In this study, we linked complex farming systems set along a landscape gradient with a factorial field-scale experiment to identify main direct and indirect drivers of winter wheat yield. Although we initially assumed top-down control across all trophic levels, resource-driven relationships were dominant in this study: yield was primarily determined by nutrient supply, pests and predators by host and prey availability, respectively. Lacking evidence of expected negative relationships between predators and pests suggests that pest control in this system is insufficient to compensate for bottom-up resource availability. Strengthening observed links between natural enemies and landscape (mean field size) or local management aspects (intensity of soil management, addition of soil organic matter, crop rotation diversity) may restore the pest control potential and lessen reductions in yield quality and quantity associated with herbivory. These ecological pathways, together with expected benefits of agrochemical reductions and improved soil quality, provide additional tools for ecological intensification. Accordingly, weak links between other ecosystem services (e.g. pollination) and yield could be fostered by future adaptive crop and landscape management. Considering the large-scale threats of conventional agriculture to biodiversity, the environment, food security and human health, anticipated, limited yield losses are an acceptable price compared to the economic and environmental benefits of a turnaround to more sustainable agriculture.

III.6 Supplement

III.6.1 Detailed description of experimental design

This research was conducted as part of a larger field experiment within the framework of the project Liberation ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificATION"), funded by the European Union (grant number: 311781). This major study explored how local management practices (fertilizer application, insecticide input, field soil organic carbon) in combination with changes in cropland area at the expense of seminatural habitat determine the abundance of pests and predators, biological pest control, and crop yields. For this purpose, a common field experiment was designed and implemented in seven European countries participating in the research (Germany, Hungary, Italy, Poland, Sweden, The Netherlands, United Kingdom).

The common experiment incorporated a paired-field design (Figure II.S1, (Gagic *et al.*, 2017)), in which pairing was achieved by joining two conventional winter wheat fields of contrasting soil organic carbon content (= SOC, high/low) yet similar soil texture, pH (less than 0.5 unit difference) and field margin quality (mostly grassy edge) along a gradient of landscape simplification defined by the proportion of seminatural habitat in 1000m radius (Table II.S1). Fields were additionally chosen to minimize correlations between seminatural habitat and other configurational (mean field size, density of field edges) and compositional (% grassland and cereal, spatial crop diversity) landscape variables (Table II.S2). A total of 28 fields (14 field pairs, within-pair distance between fields mean±SD 1.07±0.9km, range 0.19-2.5m) were selected in this manner.

The paired design allowed to separate effects of increasing soil organic carbon from those of soil texture and pH. At the same time, fields were selected to include different management practices (e.g. till or no-till, long or short crop rotations, mineral vs. organic fertilizer input) to ensure that SOC effects were not in fact driven by specific field management types. Soil conditions of potential fields were assessed by collecting five soil cores (30mm diameter, 15cm deep). Samples were pooled within fields, homogenized and stored at 5°C before analyses of pH and SOC. In Germany, soil texture within potential fields was determined using soil maps (Bayerische Vermessungsverwaltung 2010). Correlations between landscapes variables, soil characteristics and management were low (Pearson's r $|<0.5|$, Table II.S2).

Study plots (> 50x15m) were established along the edge of each field, at least 15m from headlands. A crossed insecticide (pyrethroid insecticide, yes/no) and fertilizer treatment (yes/no). The broad spectrum pyrethroid insecticide (active substance of beta-cyfluthrin = 7.5 g ha^{-1}) was applied once using backpack sprayers after the first visual arthropod count irrespective of actual pest attack rates. Fertilizer treatments comprised three applications of ammonium sulphate nitrate following regional recommendations at tillering (~BBCH 20, N = 90 kg ha^{-1}), stem elongation (~BBCH 30, N = 50 kg ha^{-1}) and heading (~BBCH 55, N = 50 kg ha^{-1}). Farmers were not allowed to use insecticides or fertilizers on or near study plots. Herbicides and fungicides were applied as usual.

III.6.1.1 Quantifying drivers of yield

Including the implemented experimental treatments insecticide and fertilizer application, 34 explanatory variables were considered as direct or indirect drivers of yield in our system. These included both abiotic and biotic drivers.

Soil characteristics

A first set of environmental variables related to the soil characteristics assessed during field selection (soil type, pH and SOC content).

Present and historic crop management

Crop management data was derived from the experimental set-up ('Nitrogen fertilizer application') and from farmer surveys performed in autumn 2014. Farmer surveys covered past (mean data availability 11.25 ± 0.43 years) and recent crop management information related to sowing and general management (Table II.S1). We aimed to include variables known (or assumed) to affect pests and natural enemies, as well as yield.

Influence of landscape heterogeneity

Landscape heterogeneity was assessed in circular areas of 1 km radius around study fields using ArcGIS v. 10.4 (ESRI) with a focus on variables relevant for pests and arthropod antagonists, including variables of landscape configuration and composition (Table II.S1). Due to the type of pests and natural enemies in this system, we especially considered the amount of alternative hosts (permanent grassland, proportion of cereal grown in the landscape) and the availability of resources and habitat (amount of seminatural habitat), as well as the spatial configuration hindering or favouring dispersal (mean field size, arable edge density).

Drivers of pest regulation

Effects of agrochemical application, landscape and management were explored by sampling leaf- and soil-dwelling predators on treatment plots using two distinct methods. Leaf-dwelling predators such as ladybirds (Coccinellidae, adults and larvae), hoverflies (Syrphidae, larvae), lacewings (Chrysopidae, larvae), and web-building spiders (Araneae) were assessed in three consecutive visual counts at stem elongation, heading and fruit development. Abundances of natural enemies were counted on 50–100 randomly selected tillers per treatment plot, then standardized to counts per 50 tillers and summed across surveys to estimate pest control potential throughout the wheat growing season. Due to differences in their response to agricultural intensification, we distinguished between leaf-dwelling predators actively dispersing as winged adults (‘active flyers’: ladybirds, hoverflies, lacewings) and wind-dispersed web-building spiders (‘passive flyers’).

We determined activity density of two groups of soil-dwelling predators, namely predatory ground beetles (Carabidae) and ground-hunting spiders (mainly Lycosidae), by placing one pitfall trap within each treatment plot (distance from edge >10m) at wheat flowering stage. Traps remained in the field for 10 days. They consisted of polypropylene beakers (155mm high, 95mm diameter) filled with 200 mL propylene glycol:water solution (ratio 1:3) and a drop of detergent to reduce surface tension. Traps were covered with roofs (20x20cm, 10cm above traps) to prevent flooding by rain.

The experimental treatment 'insecticide application' was also regarded as driver of pest regulation and therefore included in this category.

Pests and diseases

During the visual counts we also recorded the abundance of pests – aphids (Hemiptera: Sternorrhyncha) and cereal leaf beetles (Coleoptera: Chrysomelidae). Abundances were pooled across three surveys to assess the accumulated effect of pest pressure on yield across the growing season, and standardized to counts per 50 tillers. The English grain aphid *Sitobion avenae* (Fabricius) preferentially feeds on the grain, whereas the rose-grain aphid *Metopolophium dirhodum* (Walker) is mostly found on stem and leaves. Counts were therefore kept separate. Cereal leaf beetles included *Oulema melanopus* (Linnaeus) and *Oulema gallaeciana* (Heyden), yet we distinguished between larvae (sessile, '*Oulema* larvae') and adults (winged, '*Oulema* adults'), that differ in their mobility and effect on yield.

To assess effects of plant pests on insects and yield we conducted a weed survey (forbs and grasses) during fruit development of wheat within four 0.25 sqm subplots in each treatment plot. Weed pressure was then estimated as percent cover per sqm, rounded to the nearest 5%. As grass cover was low, only forb cover was used for analysis. Additionally, incidence of the pathogenic fungi *Fusarium* and rust (*Puccinia* spp.) were assessed by averaging the number of infested leaves (out of 50) recorded during two visual pathogen surveys at booting and flowering stage.

Yield components

During harvest time, 1 m-2 of wheat was hand harvested from every treatment plot (four randomly located 0.25 m-2 subplots), and grain dry weight per hectare (t ha-1) adjusted to 12% grain moisture was estimated. In addition, we determined moisture-adjusted thousand kernel weight (TKW, g) and air-dried plant biomass (without grain, kg m-2). These three yield components were treated as final response variables in our analysis.

Despite having a total of 112 plots, only 94 to 108 data points could be used for the analyses (see Table II.S3) as some of the data was incomplete (missing data of visual surveys in four treatment plots, seven plot samples of predatory carabids and 18 of ground-dwelling spiders collected with pitfall traps).

Table II.S1 Description of variables used in piecewise structural equation models (SEM), with summary statistics of continuous variables. The eleven response variables of individual path models (type 'R') also acted as explanatory variables (type 'E'), if pre-selection of fixed terms suggested possible links (see Table II.S2 & S3).

	Type	Min	Max	Mean±SE	Description
Yield components					
Yield	R/E	2.8	14.7	7.6±0.24	Grain yield (t/ha)
Biomass	R/E	0.2	1.7	0.8±0.03	Plant biomass (g) excluding grain
TKW	R/E	36.7	53.3	44.03±0.32	Thousand kernel weight (g), moisture adjusted
Pests and diseases					
Sitobion avenae	R/E	1	624	143±11.55	Aphid abundance per 50 tillers (three surveys)
Metopolophium dirhodum	R/E	0	88	7.17±1.1	Aphid abundance per 50 tillers (three surveys)
Oulema adult	R/E	0	16	1.98±0.24	Cereal leaf beetle abundance per 50 tillers (three surveys)
Oulema larva	R/E	0	42	7.32±0.74	Cereal leaf beetle abundance per 50 tillers (three surveys)
Fusarium	E	0	15	4.29±0.7	Number of infested leaves (out of 50)
Rust	E	0	25.8	5.51±1.3	Number of infested leaves (out of 50)
Weed cover	E	0	7.5	1.61±0.5	Cover of weedy forb per m^{-2}
Natural enemies					
Ground spiders	R/E	0	17	3.72±0.34	Activity density of ground-hunting spiders
Predatory carabids	R/E	1	68	3.34±0.38	Activity density of predatory carabid species
Active flyers	R/E	0	12	1.78±0.23	Abundance of flying predators actively dispersing in adult stage
Passive flyers	R/E	1	32	9.02±0.58	Abundance of wind-dispersed leaf-dwelling spiders
Insecticide application	E				Insecticide application on treatment plot (two levels: yes/no)
Soil characteristics					
Soil organic carbon	E	0.87	4.36	1.39±0.12	% SOC content (continuous)
Topsoil type	E				Three-level factor (loam, sandy loam, sandy clay loam)
Soil pH	E	6.27	7.36	6.7±0.06	Continuous predictor
Crop management					
2014					
Soil preparation	E				Intensity of soil management. Three levels: low (no-till), medium (cultivator), high (deep ploughing)

	Type	Min	Max	Mean±SE	Description
Sowing date	E				Date of wheat sowing (factor)
Seeding rate	E				Seeding rate of wheat (factor)
Previous crop	E				Crop preceding wheat in rotation (factor)
Wheat cultivar	E				Cultivar grown (factor)
Nitrogen fertilization	E				Fertilizer application on treatment plot (two levels: yes/no)
Plant growth regulator	E				Application of plant growth regulator (two levels: yes/no)
Long-term (in rotation)					
Crop rotation diversity	E	0.5	1.38	1±0.05	diversity of crop rotation preceding wheat, based on six crop groups: maize, oilseed rape, soy, sugar beet, summer cereal, winter cereal
Prop. ploughing	E	0	1	0.5±0.07	Frequency of intensive soil management (deep ploughing).
Prop. organic fertilizer	E	0	1	0.34±0.07	Frequency of organic fertilizer application
Prop. insecticide	E	0	0.8	0.23±0.04	Frequency of insecticide application
Prop. residue	E	0	1	0.77±0.05	Frequency residue remained on field
Prop. cover crops	E	0	0.4	0.16±0.03	Frequency cover crop grown
Landscape heterogeneity (1 km radius)					
Mean field size	E	0.51	4.18	1.99±0.18	Average patch size of arable fields (ha)
Arable edge density	E	59.4	201.6	126.35±6.6	Density of field edges (m ha^{-1})
Arable crop diversity	E	0.74	1.44	1.08±0.04	Landscape-level crop diversity, Shannon Wiener index based on 12 arable crop groups: cereals (excluding grain maize), 1- or 2-year old fallows, flowers and ornamental plants, temporary grassland and green fodder (green maize), legumes, maize, oilseed and fibre crops (excluding rape), rape and turnips, root crops, sunflowers, vegetables, other industrial crops (Eurostat 2012)
Prop. permanent grassland	E	0	19.6	3.06±0.79	Cover of permanent grassland (%)
Prop. seminatural habitat	E	6.36	42.64	17.52±1.97	Amount of seminatural habitat (%)
Prop. cereal	E	18.8	79.5	54.4±2.65	Proportion of cereal grown in landscape (%)

Table II.S2 Pearson's *r* correlation matrix of variables (numbered 1 to 37) used in the piecewise structural equation model, which consisted of 11 individual path models. Response variables (type 'R') of individual models also acted as explanatory variables (type 'E'), whereby we assumed top-down effects for pests on yield, and natural enemies on pests (i.e. higher trophic levels were added as fixed effects for lower trophic levels). However, if correlations were positive (suggesting bottom-up effects), the lower trophic level term was included as predictor in higher trophic level models (e.g. plant biomass as predictor of pest abundance, correlation values marked with [a]). Fixed factors were excluded from initial individual path models if relationships were weak (Pearson's *r*|<0.2|, in grey) or unsupported by ecological theory (in red). In the latter case, terms were only added if the SEM analysis suggested a missing link (marked with [b]). Full initial models listed in Table II.S3. During SEM simplification, fixed terms included in models yet non-significant were removed (black italic values), unless the removal reduced SEM fit (determined by AICc). Highlighted in bold are the remaining fixed terms of the eleven models (Table II.S3).

			Variable No.																																				
Variable	No.	Type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	No.
Yield components																																								
Grain yield	1	R/E	NA	**0.75**	0.14	**-0.45**	**0.27**[a]	*0.37*[a]	0.12	0.04	-0.03	*-0.30*	-0.11	0.20	-0.03	-0.17	0.09	-0.18	**-0.46**	-0.11	-0.02	0.09	0.06	-0.08	-0.08	**0.38**	0.17	0.05	-0.12	*0.27*	0.18	-0.19	0.17	0.34	-0.03	-0.11	0.15	0.07	0.08	1
Plant Biomass	2	R/E		NA	0.09	**-0.31**	0.13	**0.36**[a]	**0.23**[a]	0.09	-0.05	**-0.29**	-0.07	0.17	0.10	-0.14	-0.05	-0.20	*-0.33*	-0.06	-0.15	0.02	0.04	-0.05	0.08	**0.32**	0.20	-0.03	-0.01	*0.25*	0.13	**-0.29**	0.11	0.38	-0.20	-0.07	0.17	0.14	-0.05	2
Thousand kernel weight	3	R/E			NA	0.07	0.14	-0.06	**-0.21**	-0.10	0.14	-0.04	0.13	0.35	0.05	0.02	0.17	*-0.27*	-0.11	-0.02	**0.42**	0.00	-0.17	*-0.25*	-0.06	-0.04	*0.29*	**0.39**	*-0.22*	-0.17	0.31	-0.11	0.14	0.09	0.05	-0.04	-0.34	0.06	0.02	3
Pests and diseases																																								
Sitobion avenae	4	R/E				NA	-0.17	0.02	-0.02	-0.13	0.05	*0.27*	0.14	-0.08	**0.36**[a]	*0.23*[a]	-0.12	0.22	0.40	0.21	-0.08	-0.32	-0.06	-0.37	0.19	-0.11	0.02	*0.22*	0.28	-0.17	-0.05	-0.15	-0.06	**-0.42**	-0.17	0.06	-0.11	*0.30*	*-0.40*	4
Metopolophium dirhodum	5	R/E					NA	-0.02	-0.09	0.04	0.02	-0.12	0.02	*0.44*[a]	0.11	-0.14	0.03	-0.03	-0.17	-0.28	0.16	**0.39**[b]	0.05	0.03	-0.19	0.06	0.04	-0.04	-0.25	*0.24*	0.18	-0.07	0.11	*0.25*	0.01	-0.05	-0.14	-0.12	-0.06	5
Oulema adult	6	R/E						NA	**0.44**[a]	0.01	0.05	-0.06	**0.21**[a]	0.02	0.11	0.02	-0.15	-0.12	0.03	0.09	-0.07	-0.15	0.06	-0.25	-0.09	0.17	0.10	*0.23*	0.21	*0.23*	-0.07	*-0.30*	*0.37*	-0.19	*-0.22*	0.01	0.15	**0.36**	-0.14	6
Oulema larva	7	R/E							NA	0.02	-0.09	-0.12	0.10	-0.16	0.08	**0.27**	**-0.61**	-0.11	-0.08	0.03	-0.13	-0.17	0.25	-0.11	0.14	-0.01	0.05	0.08	0.16	0.03	-0.03	-0.13	0.17	-0.05	-0.20	-0.04	*0.21*	*0.21*	0.05	7
Fusarium	8	E								NA	0.21	0.01	0.10	-0.04	-0.13	-0.12	-0.08	0.07	-0.18	0.14	-0.11	0.01	-0.08	0.30	0.07	-0.03	0.03	-0.06	-0.12	0.12	0.08	0.07	-0.21	-0.09	-0.13	0.04	0.32	0.25	0.05	8
Rust	9	E									NA	0.13	0.34	0.04	0.00	0.00	-0.01	-0.12	0.19	-0.18	0.30	-0.12	-0.20	-0.17	0.13	0.03	0.01	0.18	-0.23	-0.01	0.16	0.01	0.16	-0.24	-0.42	0.07	-0.11	0.27	-0.33	9
Weed cover	10	E										NA	0.24	-0.01	0.00	0.02	0.04	0.16	0.05	-0.03	0.05	-0.16	-0.03	-0.17	-0.03	-0.13	-0.03	0.10	-0.10	0.09	0.03	0.05	0.04	-0.17	-0.05	0.19	0.00	0.01	-0.19	10
Pest regulation																																								
Ground spiders	11	R/E											NA	0.10	0.03	0.13	0.00	**0.22**	0.05	-0.12	**0.22**	*-0.22*	-0.01	-0.13	0.03	0.23	0.25	*0.25*	-0.15	0.20	0.15	**-0.27**	*0.26*	**-0.32**	**-0.34**	0.07	0.05	*0.27*	*-0.26*	11
Predatory carabids	12	R/E												NA	0.02	*-0.23*	-0.07	0.10	*-0.22*	-0.14	**0.29**	**0.39**	-0.04	-0.09	-0.14	0.08	0.13	-0.07	*-0.34*	**0.28**	*0.23*	-0.11	0.06	0.18	0.10	-0.05	-0.19	-0.06	-0.02	12
Active flyers	13	R/E													NA	*0.23*	-0.05	-0.10	-0.01	0.00	-0.13	0.02	0.33	-0.28	0.06	0.05	0.15	*0.30*	0.15	-0.05	0.14	*-0.22*	0.06	-0.03	**-0.28**	-0.10	0.05	*0.25*	-0.20	13
Passive flyers	14	R/E														NA	-0.11	-0.06	-0.03	0.14	0.09	-0.26	0.22	-0.30	0.24	0.00	-0.01	**0.34**	0.08	*-0.26*	0.10	-0.02	0.00	*-0.23*	-0.09	0.00	-0.08	0.20	-0.06	14
Insecticide application	15	E															NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15
Soil characteristics																																								
Soil organic carbon	16	E																NA	-0.18	0.18	0.09	-0.13	-0.10	0.07	-0.15	0.00	0.14	-0.38	-0.22	-0.02	0.11	0.15	-0.22	0.14	0.33	-0.07	0.09	-0.16	0.15	16
Topsoil type	17	E																	NA	0.16	-0.02	-0.14	-0.13	0.02	0.38	0.00	-0.27	0.02	0.43	-0.20	-0.21	0.03	0.03	-0.45	-0.30	0.01	-0.12	0.30	-0.41	17
Soil pH	18	E																		NA	0.03	-0.36	-0.08	0.01	0.02	0.00	0.00	-0.04	0.10	-0.26	0.07	-0.04	-0.37	-0.15	0.09	-0.17	0.27	0.29	0.17	18
Crop management																																								
Soil preparation	19	E																			NA	-0.02	-0.22	-0.15	0.00	0.00	0.37	0.13	-0.71	-0.25	0.31	0.31	0.13	0.03	0.02	-0.33	-0.19	0.01	0.07	19
Sowing date	20	E																				NA	0.18	0.33	-0.41	0.00	-0.12	-0.26	-0.11	0.21	0.02	0.07	-0.14	0.33	0.18	-0.30	-0.23	-0.24	0.17	20
Seeding rate	21	E																					NA	-0.10	0.01	0.00	0.12	0.21	0.17	-0.06	0.34	-0.06	0.00	0.00	-0.29	-0.11	0.32	0.23	0.08	21
Previous crop	22	E																						NA	-0.10	0.00	-0.23	-0.51	-0.09	-0.01	-0.22	0.17	-0.17	0.32	0.19	-0.15	0.03	-0.33	0.34	22
Wheat cultivar	23	E																							NA	0.00	-0.03	-0.02	0.04	-0.29	0.09	0.16	-0.10	-0.27	-0.33	0.05	0.14	0.39	-0.32	23
Nitrogen fertilization	24	E																								NA	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	24
Plant growth regulator	25	E																									NA	0.30	-0.38	-0.08	0.33	0.01	0.42	-0.13	0.04	-0.11	0.26	0.36	-0.20	25
Crop rotation diversity	26	E																										NA	0.11	-0.09	0.20	-0.24	0.44	-0.38	-0.20	0.18	-0.07	0.38	-0.33	26
Prop. ploughing	27	E																											NA	-0.06	-0.34	-0.22	0.00	-0.19	-0.07	0.30	-0.04	0.10	-0.24	27
Prop. organic fertilizer	28	E																												NA	-0.29	-0.44	0.27	0.15	-0.16	0.04	0.19	-0.05	-0.11	28
Prop. insecticide	29	E																													NA	0.15	-0.23	-0.04	-0.13	-0.30	0.12	0.28	0.22	29
Prop. residue	30	E																														NA	-0.10	-0.04	0.25	-0.20	0.19	-0.05	0.15	30
Prop. cover crops	31	E																															NA	-0.16	-0.13	0.07	0.05	0.26	-0.47	31
Landscape heterogeneity																																								
Mean field size	32	E																																NA	0.03	-0.25	-0.12	-0.56	0.35	32
Arable edge density	33	E																																	NA	0.28	-0.34	-0.53	0.26	33
Arable crop diversity	34	E																																		NA	-0.24	-0.28	-0.36	34
Prop. permanent grassland	35	E																																			NA	0.49	0.02	35
Prop. seminatural habitat	36	E																																				NA	-0.42	36
Prop. cereal	37	E																																					NA	37

Table II.S3 List of eleven individual path models used in the piecewise structural equation model (SEM). Given are response variables and the fixed effects of simplified final models, with removed, non-significant fixed effects of initial models in brackets. All models were linear mixed effects models with a random intercept of 'Field' nested in 'Pair' (performed in R package nlme). Interactions between a selected number of explanatory variables were assessed in preliminary analyses using simple linear mixed effects models (Table II.S4), with the aim of only including significant interactions in the SEM. However, as tested interactions were not significant, none were included in the individual path models. Residuals were checked graphically for normality and homoscedasticity. The number of data points (*n*) used for each model varies due to missing data (see Appendix S1). Marginal (only fixed effects) and conditional (marginal and random effects) *R^2* of each model are provided.

Response variable	Fixed effects	*n*	Marginal *R*^2	Conditional *R*^2
Yield	plant biomass + *Sitobion avenae* + fertilization + soil type (weed cover + proportion of organic fertilizer)	108	0.61	0.74
Thousand kernel weight	*Oulema* larvae + soil preparation + crop rotation diversity (previous crop + proportion of ploughing + plant growth regulator + SOC content)	108	0.32	0.73
Plant biomass	*Sitobion avenae* + fertilization + weed cover + frequency residue left-over (soil type + proportion of organic fertilizer)	108	0.28	0.71
Sitobion avenae	mean field size (crop rotation diversity + seminatural habitat cover + weed cover + proportion of cereal grown)	108	0.11	0.69
Metopolophium dirhodum	yield, sowing date (proportion of organic fertilizer + mean field size)	108	0.27	0.37
Oulema adults	plant biomass + seminatural habitat cover (proportion of cover crops + proportion of residue + arable edge density + yield + proportion of organic fertilizer + crop rotation diversity)	108	0.22	0.43
Oulema larvae	*Oulema* adults + insecticide application (seminatural habitat cover + plant biomass + proportion of grassland)	108	0.45	0.69
Ground-dwelling spiders	SOC content + soil preparation + frequency residue left-over + arable edge density + mean field size (*Sitobion avenae* + sowing date + nitrogen fertilizer + proportion of cereal + crop rotation diversity + proportion of cover crops + seminatural habitat cover)	94	0.38	0.41
Predatory carabids	soil preparation + frequency of organic fertilization (*Metopolophium dirhodum* + soil type + passive flyers + proportion of ploughing + proportion insecticide)	105	0.33	0.62
ActFly	*Sitobion avenae* + arable edge density (*Metopolophium dirhodum* + passive flyers + proportion of residues + proportion of cover crops + crop rotation diversity + seminatural habitat cover)	108	0.2	0.37
PasFly	crop rotation diversity + *Oulema* larvae (*Sitobion avenae* + proportion of organic fertilizer + mean field size)	108	0.19	0.62

Table II.S4 Interactive effects assessed in preliminary analyses using simple linear mixed effects models with the random term 'Field' nested in 'Pair'. Aim was to only include interactions in the SEM that were found to be significant in these analyses. Interactions were tested for the response variables grain yield, plant biomass, thousand kernel weight (TKW), ground spiders and predatory carabids, with explanatory variables related to soil characteristics (soil type, SOC content) and fertilization practices (nitrogen fertilization, frequency of organic fertilizer application). For each response variable, separate models testing listed interactions were run (30 models in total). As none of the interactions were found to be significant, individual component path models only included main effects (Table II.S2). All models were graphically validated for normality and homogeneity of variance.

Response	Fixed effects and interactions tested
yield/ biomass/ thousand kernel weight/ ground spiders/ predatory carabids	SOC + soil type + SOC x soil type
	SOC + fertilization + SOC x fertilization
	SOC + frequency of organic fertilizer application + SOC x frequency of organic fertilizer application
	soil type + frequency of organic fertilizer application + soil type x frequency of organic fertilizer application
	soil type + Fertilization + soil type x fertilization
	fertilization + frequency of organic fertilizer application + fertilization x frequency of organic fertilizer application

Table II.S5 Results of structural equation model combining eleven individual path models (Table II.S2). Given are standardized coefficients (estimates), standard error (SE), P-values and significance ((*)P<0.1, *P<0.05, **P<0.01, ***P<0.001)) for each path.

Response variable	Predictor variable	Estimate	SE	*P*-value	
Yield	Plant biomass	0.43	0.08	<0.001	***
Yield	Nitrogen application	0.46	0.11	<0.001	***
Yield	*Sitobion avenae*	-0.19	0.07	0.011	*
Yield	Soil type (loam vs sand)	-0.65	0.23	0.013	*
Yield	Soil type (loam vs. clay)	-0.41	0.32	0.227	
Thousand kernel weight	Soil preparation (Low vs. High)	-0.99	0.31	0.008	**
Thousand kernel weight	*Oulema* larvae	-0.16	0.06	0.009	**
Thousand kernel weight	Crop rotation diversity	0.34	0.13	0.030	*
Thousand kernel weight	Soil preparation (Medium vs. High)	0.02	0.25	0.935	
Plant biomass	Nitrogen application	0.59	0.10	<0.001	***
Plant biomass	*Sitobion avenae*	-0.22	0.09	0.014	*
Plant biomass	Weed cover	-0.15	0.06	0.017	*
Plant biomass	Frequency residue left-over	-0.35	0.14	0.024	*
Sitobion avenae	Mean field size	-0.33	0.16	0.068	(*)
Metopolophium dirhodum	Yield	0.37	0.09	<0.001	***
Metopolophium dirhodum	Sowing date	0.33	0.10	0.005	**
Oulema adults	Plant biomass	0.35	0.09	<0.001	***
Oulema adults	Seminatural habitat	0.27	0.13	0.048	*
Oulema larvae	Insecticide application	-1.27	0.11	<0.001	***
Oulema larvae	*Oulema* adults	0.14	0.07	0.050	*
Ground spiders	Arable edge density	-0.32	0.09	0.009	**
Ground spiders	Soil organic carbon content	0.36	0.11	0.012	*
Ground spiders	Soil preparation (Low vs. High)	-0.76	0.25	0.016	*
Ground spiders	Mean field size	-0.29	0.10	0.017	*
Ground spiders	Frequency residue left-over	-0.28	0.09	0.019	*
Ground spiders	Soil preparation (Medium vs. High)	-0.25	0.20	0.256	
Predatory carabids	Soil preparation (Low vs. High)	-1.03	0.34	0.013	*
Predatory carabids	Sowing date	0.37	0.13	0.015	*
Predatory carabids	Frequency organic fertilizer	0.32	0.13	0.031	*
Predatory carabids	Soil preparation (Medium vs. High)	-0.20	0.28	0.498	
Active flyers	*Sitobion avenae*	0.41	0.10	<0.001	***
Active flyers	*Metopolophium dirhodum*	0.25	0.09	0.006	**
Active flyers	Arable edge density	-0.25	0.11	0.047	*
Passive flyers	*Oulema* larvae	0.28	0.07	<0.001	***
Passive flyers	Crop rotation diversity	0.33	0.14	0.032	*

* Abundance of *Sitobian avenae, Metopolophium dirhodum, Oulema* (adults and larvae), active and passive flyers, and activity density of ground-dwelling spiders and predatory carabids log-transformed

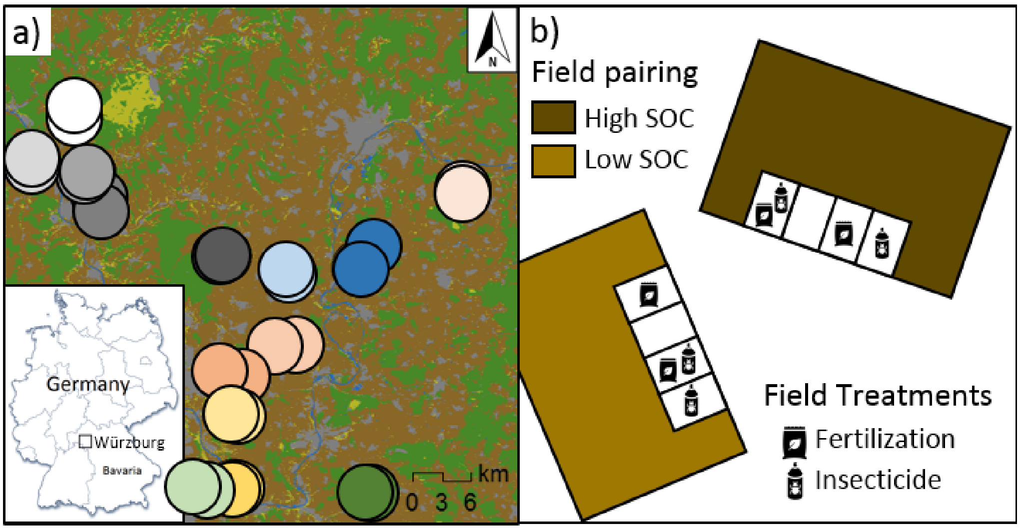


Figure II.S1 Experimental set-up of field experiment in winter wheat near Würzburg, Germany (49°47` N, 9°57` E). (a) 14 field pairs (colored circles) were selected along a gradient of landscape complexity (seminatural habitat cover). Shown are 3 km radii around fields. (b) Each pair comprised two fields of contrasting soil organic matter content (high/low). Fertilizer (no/yes) and insecticide treatments (yes/no) were applied on the subplot scale.

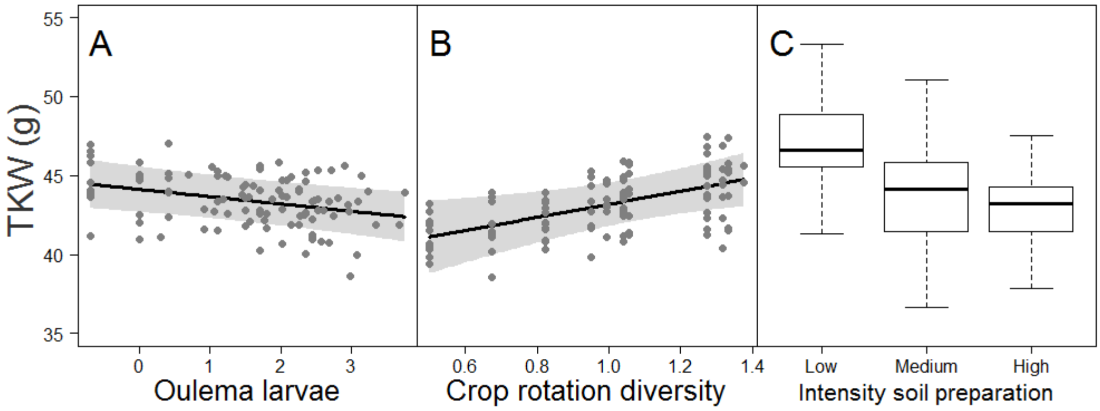


Figure II.S2 Main direct drivers of thousand kernel weight (TKW). Effects of *Oulema* larvae abundance (A), crop rotation diversity (B) and soil preparation (C, 'Low' = no-till, 'Medium' = surface cultivation, 'High' = deep ploughing). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown.

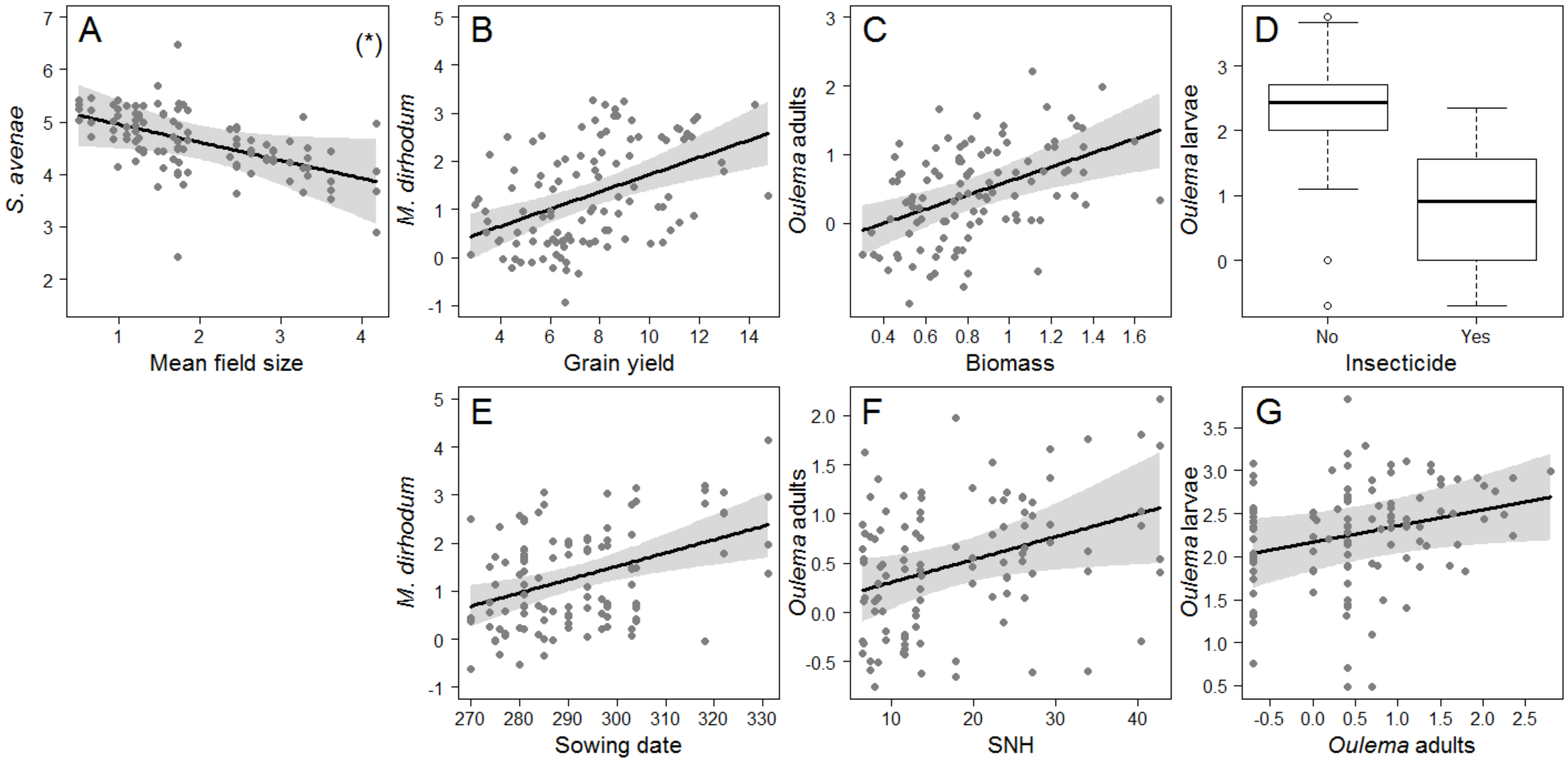


Figure II.S3 Main direct drivers of pest abundances (log-transformed). Relationships of mean field size (ha) with *Sitobion avenae* (A), grain yield (t ha^{-1}) and sowing date with *Metopolophium dirhodum* (B, E), plant biomass (kg m^{-2}) and seminatural habitat (%) with *Oulema* adults (C), insecticide application and *Oulema* abundance with *Oulema* larvae (D). For continuous variables, partial residuals, prediction lines and 95% confidence bands are shown. (*) marginally significant relationship.

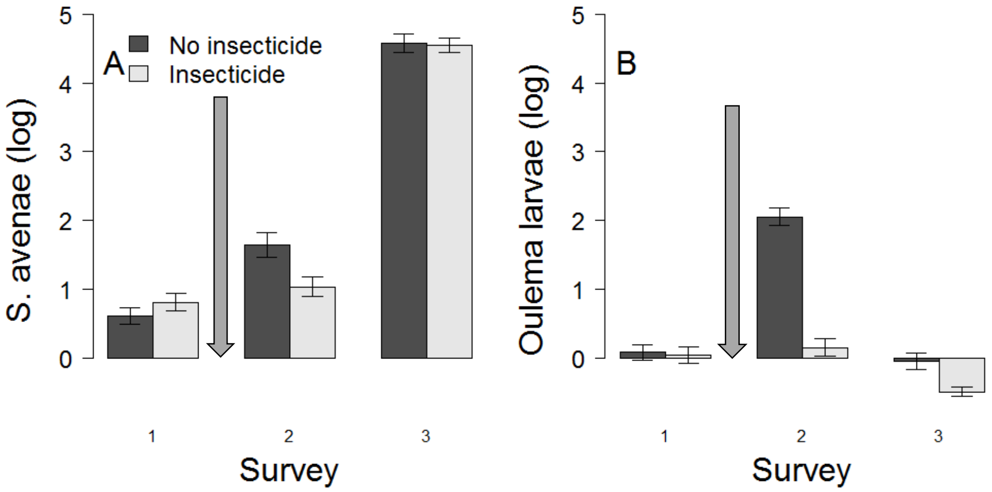


Figure II.S4 Effects of insecticide application and survey round (three levels) on abundances of *Sitiobion avenae* (A) and *Oulema* larvae (B). Pyrethroid insecticide was applied between survey round one and two, as indicated by the arrows. Additional models using distinct survey rounds and Tukey post hoc tests with FDR correction showed significant effects for both S. avenae (Survey 1: *P* = 0.22, Survey 2: *P* < 0.001, Survey 3: *P* = 0.822) and *Oulema* larvae (Survey 1: *P* = 0.99, Survey 2: *P* < 0.001, Survey 3: *P* = 0.026). No effect was observed for *Metopolophium dirhodum, Oulema* adults and the two groups of leaf-dwelling predators (active and passive flyers) in additional models testing for effects of survey round.

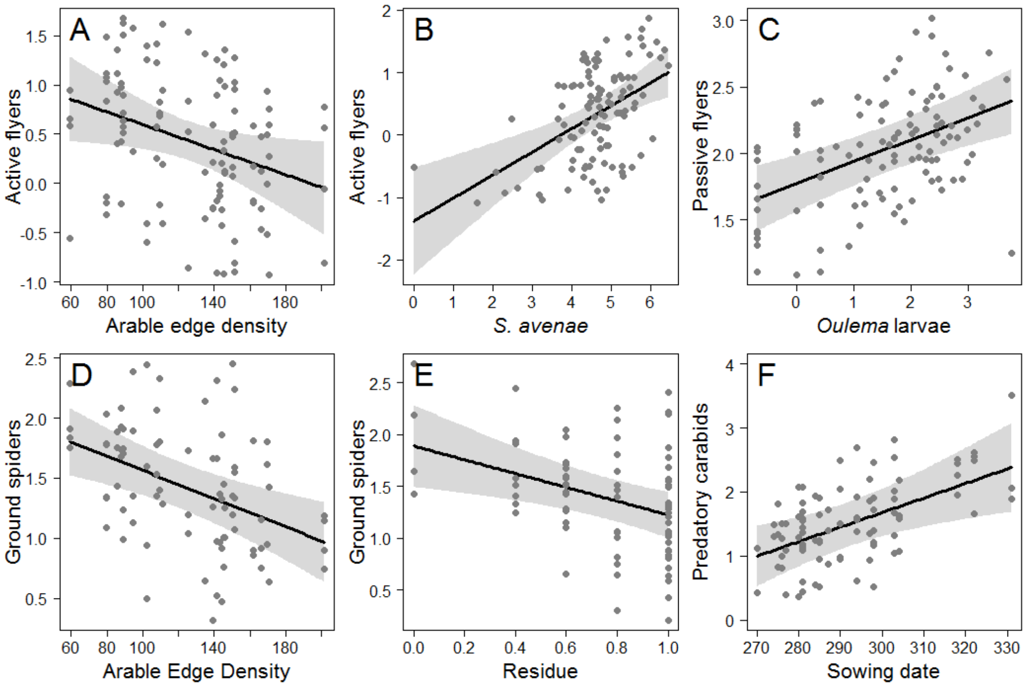


Figure II.S5 Main direct drivers of predator abundances and activity densities. Relationships of active flyers (primarily syrphid larvae and ladybirds) with arable edge density and *Sitobion avenae* (A+B), passively dispersed leaf-dwelling spiders and *Oulema* cereal leaf beetle larvae (C), ground-hunting spiders with arable edge density and frequency of residue left-over (D+E), and predatory carabids with sowing date (F). Partial residuals, prediction lines and 95% confidence bands are show

Chapter III

Landscape-level crop diversity benefits biological pest control

Landscape-level crop diversification is a promising tool for ecological intensification, whereby biodiversity and ecosystem services are enhanced, and pesticide applications reduced. Yet evidence for the effects of crop diversity at multiple scales and in different landscape contexts is lacking. Here, we investigate the potential benefits and context-dependencies of multiscale crop diversity on natural enemies and overall biological control in winter wheat. Simultaneously, we examine the mediating effects of bird predation on aphid regulation in this system. Eighteen conventional winter wheat fields were selected along two independent gradients of crop diversity and seminatural habitat cover (SNH). We assessed biological control using a natural enemy exclusion experiment ('Open Treatment', 'Bird Exclosure', 'Full Exclosure'). Biological control, predator and parasitoid densities within cages were analysed as functions of landscape (crop diversity x SNH), bird predation (yes/no) and temporal change (three surveys) on six spatial scales (100-3000 m). Crop diversity rather than SNH enhanced aphid regulation in our study system. Biological control in fields with high landscape-level crop diversity was 8 to 33 % higher than in low diversity landscapes, with main effects observed on scales <500 m. Predator and parasitoid densities increased with crop diversity on small (100–250m) and large (2000-3000 m) spatial scales, respectively. Nevertheless, our findings suggest that natural enemies other than birds, parasitoids and aerial arthropods facilitated biological control. Our study shows that landscape-level crop diversification can improve biological control in agroecosystems. Therefore, increased crop diversity could lower dependence on insecticides while enhancing yield stability through ecological intensification of farming. We also highlight the need to assess biological control rather than natural enemy abundances to avoid bias due to sampling artefacts or species interactions. Lastly, simple measures of crop diversity (e.g. 'effective number of crop types') help in science communication and the development of farm management guidelines.

III.1 Introduction

Worldwide, natural enemy communities and biological pest control suffer from increased homogenization of food production and the removal of natural habitats (Altieri, 1999; Rusch *et al.*, 2016). In addition, replacement of biological control agents with chemical insecticides results in long-term risks (biodiversity loss, pesticide resistance, groundwater contamination) that largely outweigh the perceived short-term yield and cost benefits (Wilson & Tisdell, 2001). However, ecological intensification practices such as field-scale diversification via flower plantings (Letourneau *et al.*, 2011; Gurr *et al.*, 2016), and extensification of agricultural processes (pesticide reductions; (Jonsson *et al.*, 2012)) can enhance natural enemies and biological control (Bommarco *et al.*, 2013). Scaling up, landscape complexity (e.g. the quantity of seminatural habitat; (Schmidt *et al.*, 2003; Gardiner *et al.*, 2009; Chaplin-Kramer & Kremen, 2012)) and interannual changes in host plant cover (Schneider *et al.*, 2015; Bosem Baillod *et al.*, 2017) also contribute to biological control. It is yet unclear whether increasing the number of crop types cultivated within a landscape has similar benefits.

In theory, landscape-level crop diversification (hereafter 'crop diversity') should enhance natural enemies by providing diverse plant-derived resources such as pollen, nectar and shelter throughout the year (Fahrig *et al.*, 2011; Schellhorn *et al.*, 2015). Biological control can thereby be sustained in landscapes where non-crop resources are scarce (Martin *et al.*, 2016; Tscharntke *et al.*, 2016). Furthermore, crop diversity precludes yield losses due to cropland conversion or plant competition common to small-scale diversification practices (Lin 2011), while enhancing global food security and resilience against climate change via functional redundancy of beneficial organisms (Lin, 2011; Bommarco *et al.*, 2013; Aguilar *et al.*, 2015; Schellhorn *et al.*, 2015). Nevertheless, few studies explore the link between crop diversity and natural enemy density or richness (e.g. (Palmu *et al.*, 2014; Fahrig *et al.*, 2015)). Even fewer do so for the biological control service these organisms provide (Chaplin-Kramer & Kremen, 2012; Holland *et al.*, 2012; Bosem Baillod *et al.*, 2017), although the mostly positive relationship between enemy diversity and biological control (Altieri, 1999; Harrison *et al.*, 2014) can be disrupted by antagonistic species interactions (Straub *et al.*, 2008; Letourneau *et al.*, 2009).

Whether and at which spatial scale biological control responds to crop diversity depends on the specialization, life-history and movement capability of different natural enemy guilds, and their relative importance to pest suppression (Chaplin-Kramer *et al.*, 2011; Rusch *et al.*, 2013; Shackelford *et al.*, 2013; Henri *et al.*, 2015; Martin *et al.*, 2016). For example, specialist natural enemies (e.g. parasitoids) often respond to smaller spatial scales than large-bodied generalists (Chaplin-Kramer *et al.*, 2011). In systems with parasitoid-mediated biological control, landscape complexity at small spatial scales can therefore enhance pest suppression (Schmidt *et al.*, 2003). Yet the relative importance of specialist parasitoids, epigeal or aerial arthropod predators and insectivorous birds is highly disputed and varies among systems (Schmidt *et al.*, 2003; Caballero-López *et al.*, 2012; Holland *et al.*, 2012; Martin *et al.*, 2013; Rusch *et al.*, 2013; Tamburini *et al.*, 2015; Dainese *et al.*, 2017). At the same time, crop diversity benefits might only emerge in resource-depleted, simplified landscapes with low seminatural habitat cover. Here, crop diversification adds essential resources otherwise lacking in the non-crop matrix (Tscharntke *et al.*, 2005; Josefsson *et al.*, 2017). However, correlations between crop diversity and seminatural habitat often impede our ability to infer causal relationships (Fahrig *et al.*, 2011, 2015). Disentangling the independent and interacting effects of both variables across multiple spatial scales is of prime importance – both for separate natural enemy guilds and overall biological control.

Owing to differences in the mobility and specialization of natural enemies, cereal-aphid-antagonist food webs in temperate agroecosystems are well suited for multiscale landscape studies on biological control. Aphids (Hemiptera: Sternorrhyncha), most notably the species *Sitobion avenae* (Fabricius), are major pests in these systems (Dedryver *et al.*, 2010). The suite of associated natural enemies ranges from specialized biological control agents such as parasitoids (Hymenoptera, Parasitica) and ladybird larvae (Coleoptera: Coccinellidae) to generalist predators such as ground beetles (Coleoptera: Carabidae) and spiders (Araneae, various families). Additionally, insectivorous birds can suppress pests, but might also constrain insect-mediated biological control via intraguild predation on intermediate predators (Mooney *et al.*, 2010; Martin *et al.*, 2013). In cereal systems, this so-called omnivorous intraguild predation is potentially more disruptive than coincidental intraguild predation (intermediate predators consuming parasitoid larvae with their aphid host) due to large differences in body size (Straub *et al.*, 2008).

In this study, we aimed to gain a comprehensive understanding of the potential benefits and context-dependencies of multiscale crop diversity in conventional winter wheat systems. We used repeated pest and natural enemy surveys within a natural enemy exclusion experiment to evaluate the link between crop diversity and biological pest control, while testing for interacting effects with seminatural habitat cover across six spatial scales (100 to 3000 m radii around fields). Additionally, the complex natural enemy community in this system allowed us to evaluate the individual contribution of different natural enemy guilds to biological control, and their response to crop diversity. We hypothesized that crop diversity increases overall biological control (i) and the density of arthropod natural enemies (ii), yet these benefits depend on spatial scale and natural enemy guild (parasitoids vs. predators). We further assumed that crop diversity effects are most pronounced in landscapes with low seminatural habitat cover (low landscape complexity) (iii). Lastly, we assessed whether natural enemy guilds differ in their contribution to overall biological control (iv), and whether insectivorous birds constrain biological control by affecting arthropod enemies and their ability to suppress aphids (v).

III.2 Materials and Methods

III.2.1 Study area and experimental design

The study took place in an intensively cultivated region of *c.* 40 x 40 km in Lower Franconia/Germany (49°47` N, 9°57` E), an area dominated by high-input crops such as cereal, sugar beet and maize. Here, we selected 18 conventional winter wheat fields along independent gradients of crop diversity and seminatural habitat at six spatial scales. The research was conducted within the project LIBERATION ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificATION“), which explored the interactive effects of landscape simplification and local management on pests and antagonists. Following the joint design (Figure III.1, Supplement II.6.1 in Supporting Information), fields were grouped in nine pairs of contrasting soil organic carbon content (= SOC, high/low). A fertilizer treatment (yes/no) was applied in two experimental subplots at the field edge. Both SOC and fertilization might influence pests and natural enemies, yet these relationships and effects on yields are investigated elsewhere (Gagic *et al.*, 2017). We nevertheless accounted for both factors in the statistical analyses. However, pest densities (preliminary analyses), natural enemies and biological control were unaffected by SOC and fertilization in our exclusion experiment (Table III.1, Figure III.S1, Supplement II.6.1). This corroborates previous studies related to the grain aphid *Sitobion avenae* (Garratt *et al.*, 2010) and biological control (van Gils *et al.*, 2016). Hence, local management factors are not discussed further.

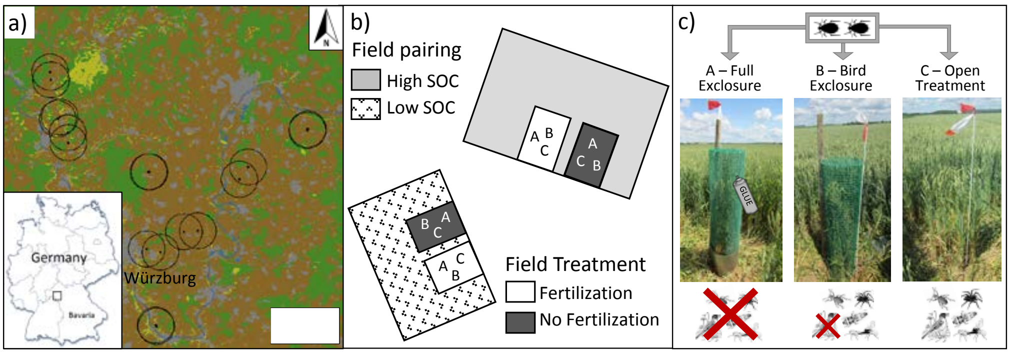


Figure III.1 Experimental set-up of the natural enemy exclusion experiment in winter wheat using sentinel aphid populations of *Sitobion avenae*. a) Nine field pairs were selected along independent gradients of crop diversity and seminatural habitat cover in central Germany. Shown are 3 km radii around fields. b) Each pair comprised two fields of contrasting soil organic matter content (high/low). Fertilizer treatments (no/yes) were applied on the subplot scale. c) Each subplot received three exclusion treatments: 'Full Exclosure' (all natural enemies excluded), 'Open Treatment' (all natural enemies present), and 'Bird Exclosure'.

III.2.2 Landscape variables

Crop diversity (CropDiv, overall range 0 – 1.48) was calculated on six spatial scales (100, 250, 500, 1000, 2000, 3000 m radii around fields) as Shannon Wiener Index in the 'vegan' package in R (Oksanen *et al.*, 2015). The index used 12 arable crop categories provided by the Bavarian State Ministry of Nutrition, Agriculture and Forestry: cereals, 1- to 2-year fallows, cultivated flowers, temporary grassland, legumes, maize, oilseed rape, root crops, sunflower, vegetables and other industrial crops (Table III.S1). To ease interpretation of CropDiv, we also calculated the 'effective number of crops' using exp (CropDiv) (= ENCS, Table III.S1; (Jost, 2006)). ENCS estimates the number of equally abundant crop types required to achieve a specific amount of CropDiv and associated levels of biological control. We use ENCS to illustrate diversification effects in a way that improves communication of research results to farmers and policy makers, and helps in the development of farm management guidelines.

Seminatural habitat cover (= SNH, overall range 1.2 – 76.9 %) included perennial grassland, orchard meadows, hedgerows, forest edges, and grass margins along rivers and roads. SNH was calculated in ArcMap v. 10 (ESRI 2011) using official digital topological maps ATKIS DTK 25 (Bayerische Vermessungsverwaltung, 2010)(Table III.S1). Correlations of CropDiv with SNH and other influential landscape factors not included in analyses (crop cover (Caballero-López *et al.*, 2012), field size (Fahrig *et al.*, 2015), and habitat diversity (Gardiner *et al.*, 2009; Martin *et al.*, 2016)) were low at all spatial scales (Pearson's $|r| \leq 0.51$, Table III.S2).

III.2.3 Biological control

Overall levels of biological control and the influence of bird predation on aphid suppression were assessed with a natural enemy exclusion experiment (Figures. III.1b & III.1c, Appendix S1). Three standardized populations of *Sitobion avenae* were established in each fertilization subplot (initial aphid density ~ 100). We then exposed populations to one of three exclusion treatments: 'Open Treatment' (aerial and epigeal invertebrate predators, parasitoids and birds), 'Bird Exclosure' (birds excluded) and 'Full Exclosure' (all natural enemies excluded). Aphid densities in each exclusion treatment (total $n = 108$, 6 cages per field) were recorded non-destructively on ten randomly selected tillers in 5-day intervals (days 0, 5, 10, 15). We estimated the overall level of biological control attributable to natural enemies by comparing 5-day aphid growth rates in treatments allowing access to some or all natural enemies ('Open Treatment', 'Bird Exclosure') with growth rates in the baseline treatment ('Full Exclosure') of the same subplot. This biological control index (= BCI; Appendix S1, (Gardiner *et al.*, 2009)) ranges from zero (no pest suppression) to one (high pest suppression). Negative values were set to zero

(Gardiner *et al.*, 2009). The index was calculated separately for 'Open Treatments' and 'Bird Exclosures', thereby yielding 216 BCI estimates (two treatments x two subplots x 18 fields x three 5-day survey intervals). The difference in BCI between the two open treatments was used to investigate the effect of birds on biological control.

III.2.4 Sampling of arthropod enemies

Biological control relates to a variety of biodiversity components (Harrison *et al.*, 2014). One such component, natural enemy richness, can negatively affect pest suppression via antagonistic species interactions (Straub *et al.*, 2008; Letourneau *et al.*, 2009). While we specifically tested for bird intraguild predation by manipulating taxonomic richness of predator groups, we otherwise aimed to avoid this potential bias by using the abundance of arthropod enemies instead. Furthermore, enemy abundance drives the magnitude of biological control, whereas species richness is mostly thought to increase the stability of this ecosystem service (Shackelford *et al.*, 2013; Harrison *et al.*, 2014). We recorded the density of leaf-dwelling natural enemies on ten randomly selected tillers during the last three aphid surveys. Due to the low occurrence of individual subgroups, all arthropod predators were pooled across families ('predator density' for days 5, 10, 15). To avoid double counting, we used the number of parasitized aphids on day 15 as estimate of parasitoid density (Shackelford *et al.*, 2013). This allowed us to compare the effect of CropDiv on large arthropod predators and small specialist parasitoids, assess their contribution to overall biological control and potential mediating effects of bird predation via intraguild predation.

III.2.5 Statistical analysis

We assessed the scale-dependent and landscape-specific effect of CropDiv on overall BCI (hypotheses i + iii) by building separate linear mixed effect models with Gaussian error distribution for each spatial scale (Table III.S3). We concurrently tested for the contribution of bird predation to BCI (hypothesis v), and temporal delays in CropDiv effects. Therefore, explanatory variables for each scale-specific landscape model were CropDiv, SNH, bird exclusion (yes/no), CropDiv x SNH and CropDiv x survey. We controlled for fertilization (yes/no) and SOC (low/high) by adding both factors as covariates. All models used a nested random structure (Pair/Field/Subplot/Cage).

Effects of CropDiv, SNH and bird predation on predator and parasitoid densities (hypotheses ii, iii + v) were analysed with a similar model structure by fitting generalized linear mixed effects models with Poisson error distribution (Table III.S3). These landscape models also accounted for aphid density (fixed term). No temporal effects were investigated for parasitoid densities (data restricted to day 15). Using parasitism rate as response yielded similar results ($\text{aphids}_{\text{parasitized}}$ /$\text{aphids}_{\text{total}}$, binomial error distribution), therefore only the effects on parasitoid densities are shown to improve comparability with arthropod predators.

Two additional linear mixed effect models (Gaussian distribution) investigated the influence of predator and parasitoid densities on BCI (hypothesis iv, Table III.S4). Potential modulating effects of bird predation (hypothesis v) and changes over time (predator model only) were assessed by including interactions with bird exclusion and survey date.

All continuous explanatory variables were z-standardized. Normality and homoscedasticity of model residuals was validated graphically. We found no significant overdispersion in Poisson models (P-values > 0.12) or multicollinearity of independent variables (variance inflation factors < 3; (Zuur *et al.*, 2009)). Residual spatial dependence was rejected for all models (P-values > 0.19, Moran's I test). We calculated marginal (fixed effects) and conditional (random and fixed effects) coefficients of determination (R^2) to assess overall model fit (Tables III.S3 - III.S5; function 'r.squaredGLMM'; (Nakagawa & Schielzeth, 2013)). Full landscape models with the highest R^2 indicate the spatial scale with the greatest predictive value. Marginal model fit (average across all scales ± SE) was reasonably high for all landscape models (BCI: 0.21±0.01, predator density: 0.23±0.01, parasitoid density: 0.3±0.03), and for models relating predator and parasitoid densities to BCI ($R^2 = 0.2$ and $R^2 = 0.13$, respectively).

We employed an information-theoretic approach (Burnham & Anderson, 2002) to quantify the strength of alternative competing models with Δ AICc < 7 (Burnham *et al.*, 2011). Model averaging across the model sets yielded estimates with associated confidence intervals (95% CIs), and the sum of Akaike weights ($\sum w_i$) for each predictor variable (Tables III.S5 & III.S6). $\sum w_i$ (range 0 to 1) can act as indicator of relative variable importance, yet due to some controversy relating to its use we focus on effects where 95% CIs of estimates exclude zero (Galipaud *et al.*, 2014). All analyses were performed using the packages 'nlme' (Pinheiro *et al.*, 2016), 'lme4' (Bates *et al.*, 2015), 'MuMIn' (Barton, 2013), 'ape' (Paradis *et al.*, 2004), and 'base' implemented in R v.3.2.2 (R Development Team, 2016).

III.3 Results

Over the 15-day survey period, we counted 65 601 aphids across all exclusion treatments. Of the 576 natural enemies recorded, the majority were aerial or vegetation-dwelling predators such as Coccinellidae (adults 28.5%, larvae 13.9%), Araneae (26.7%, mostly Linyphiidae) and Syrphidae (larvae 12.7%). On day 15, the number of parasitized aphids observed in cages ranged from zero to ten (mean±SE 'Bird Exclosure' 1.17±0.43, 'Open Treatment' 1.47±0.03). Mean aphid densities in cages without natural enemies ('Full Exclosures' 250.67±17.49) were 3.13 times higher than in 'Bird Exclosures' (80.03±8.92), and 2.29 times higher than in 'Open Treatments'(109.42±12.01). This difference, and consequently estimates of BCI, increased over time (Figures. III.2 & III.S2).

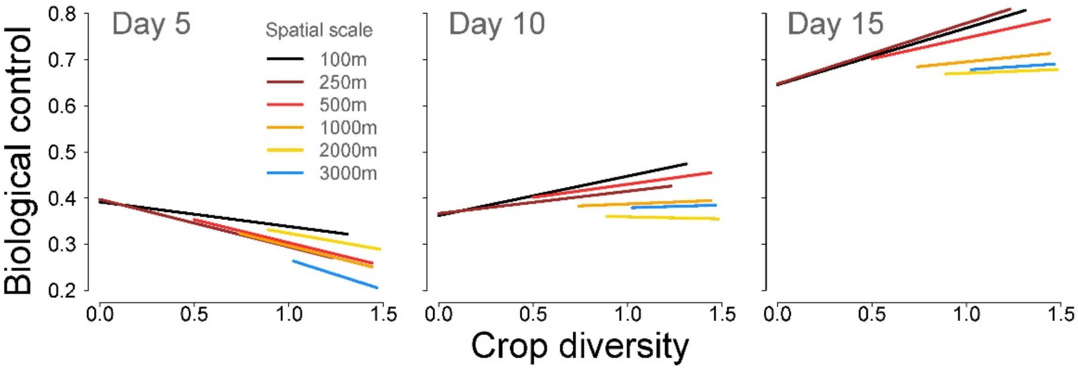


Figure III.2 Multiscale effects of crop diversity on biological control estimated for day 5, 10 and 15 of the natural enemy exclusion experiment. Regression lines show predicted results based on model-averaged estimates (including models with Δ AICc < 7).

III.3.1 Scale-dependent crop diversity effects

The benefits of CropDiv to BCI varied with time and scale considered (Figures. III.2 & III.3, Table III.1). Across all landscapes, BCI correlated negatively with CropDiv in the first survey period (day 0 to 5, Figures III.2a & III.3a). However, in subsequent surveys this relationship reversed (CropDiv x survey interaction). CropDiv on small spatial scales (100, 250 and 500 m) had the strongest positive effect on BCI, which weakened with increasing spatial scale (Figures III.2b, III.2c & III.3a). Translated to ENCS, an increase from one to three dominating crop types at the most predictive 250 m scale (highest R^2) equated to an average 33% rise in biological control (Figure III.4). In contrast, a similar increase in CropDiv at 2000 m scale (second highest R^2) only improved BCI by around 8%. Due to the contrasting relationships over time, high diversity landscapes (CropDiv > 1.38, ENCS > 4) showed the strongest temporal increase in BCI, which more than tripled over the 15-day survey period (BCI means (±SE) across all spatial scales: day 5 = 0.18 ± 0.04, day 10 = 0.32 ± 0.04, day 15 = 0.76 ± 0.03, Figure III.2).

The density of arthropod predators increased over time and with CropDiv at small spatial scales (100 m & 250 m, Figure III.3c, Table III.1). Large-scale CropDiv also positively affected parasitoids (2000 m & 3000 m, Figure III.3e, Table III.1). In addition, both natural enemy groups showed strong density-dependence with aphids (Table III.1, Figures III.S1b & III.S1c).

Table III.1 Sum of model weights ($\sum w_i$) of predictor variables included in scale-specific models for biological control (BCI), predator (PR) and parasitoid (PA) density. Predictor variables were crop diversity (CropDiv), seminatural habitat cover (SNH), survey interval (S), bird exclusion (B), and interactions of CropDiv with survey and SNH. Covariates included aphid densities (A), fertilization treatment (F) and field soil organic matter content (SOC). Bold numbering signifies $\sum w_i$ where 95 % confidence intervals of estimates excluded zero. Parenthesis highlight the presence of interactions. Hyphens indicate predictor variables not included in the full model.

	Scale																	
	100 m			250 m			500 m			1000 m			2000 m			3000 m		
	Response			Response			Response			Response			Response			Response		
	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA	BCI	PR	PA
Predictor variables																		
CropDiv	(1)	**0.99**	0.29	(1)	**0.86**	0.26	(1)	0.55	(0.69)	(0.94)	0.31	0.32	(0.79)	0.33	**0.92**	(0.98)	0.3	**0.55**
SNH	0.29	0.61	0.24	0.31	0.53	0.26	0.42	0.4	(0.73)	0.57	0.29	0.29	0.62	0.33	0.34	0.59	0.37	0.26
S*	(1)	**1**	-	(1)	**1**	-	(1)	**1**	-	(1)	**1**	-	(1)	**1**	-	(1)	**1**	-
B	0.47	0.32	0.22	0.44	0.25	0.32	0.48	0.31	0.3	0.46	0.31	0.32	0.43	0.31	0.29	0.44	0.31	0.22
Interactions																		
CropDiv: SNH	0.09	0.15	†	0.07	0.11	0.04	0.22	0.07	**0.6**	0.13	0.05	0.04	0.13	0.06	0.14	0.28	0.04	0.04
CropDiv: S*	**0.99**	0.64	-	**1**	0.19	-	**1**	0.07	-	**0.91**	0.04	-	**0.65**	0.03	-	**0.97**	0.03	-
Covariates																		
A	-	**1**	**1**	-	**1**	**1**	-	**1**	**1**	-	**1**	**1**	-	**1**	**1**	-	**1**	**1**
F	0.3	0.26	0.25	0.26	0.3	0.32	0.28	0.27	0.34	0.28	0.27	0.35	0.29	0.27	0.25	0.31	0.27	0.25
SOC	0.3	0.36	0.36	0.25	0.37	0.35	0.25	0.36	0.34	0.3	0.31	0.39	0.28	0.31	0.36	0.27	0.31	0.35

* Temporal effects of survey interval not tested for parasitoid density (data restricted to day 15)

† Interaction not selected in models with Δ AICc ≤ 7

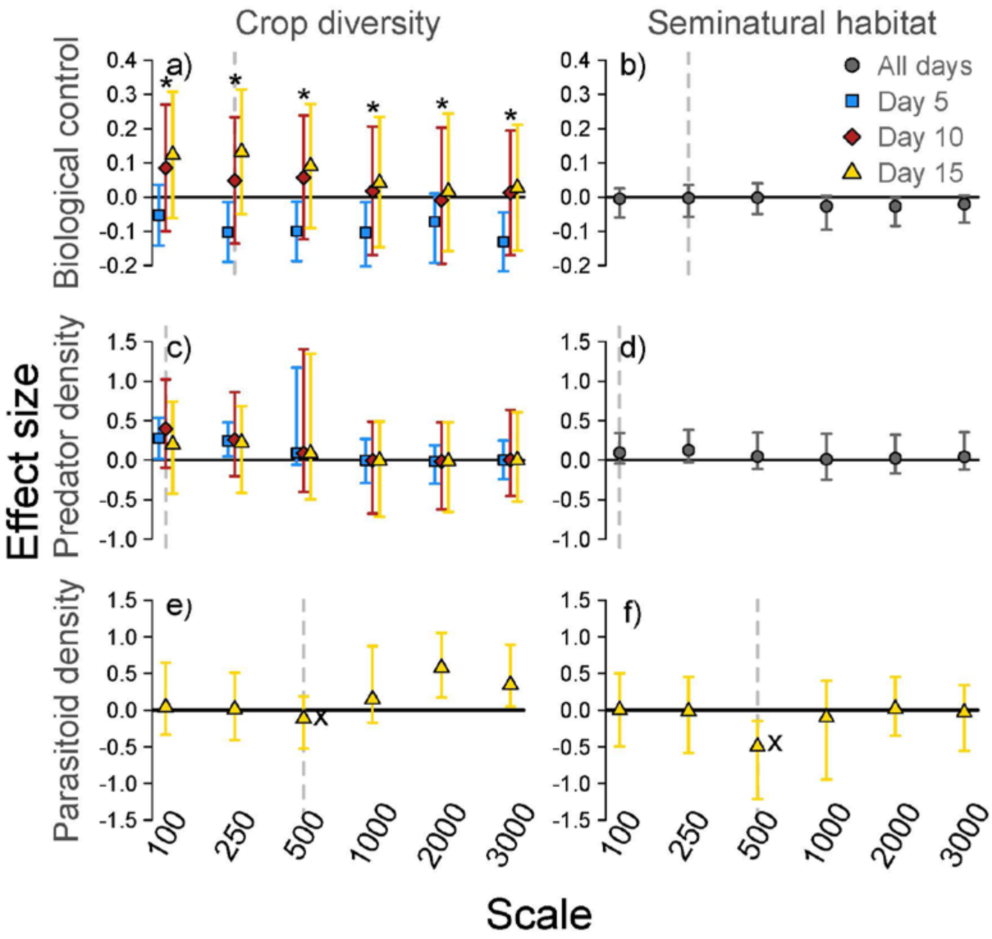


Figure III.3 Effect of crop diversity (CropDiv) and seminatural habitat (SNH) on biological control (a, b), predator (c, d) and parasitoid density (e, f) at six spatial scales. Values are model-averaged estimates ± 95% confidence intervals (Δ AICc < 7). CIs excluding zero indicate effect sizes with strong support. In biological control and predator models estimates were calculated for separate survey intervals for CropDiv or across survey intervals for SNH. Estimates for parasitoid density were calculated for day 15 only. Effect sizes > zero indicate a positive regression slope between standardized landscape predictors and response variables (positive effect). Estimates of CropDiv x survey and CropDiv x SNH interactions with CIs excluding zero are marked with asterisks and 'x', respectively, yet only estimates of main landscape effects are shown here. The most predictive scales (highest R^2 values of the full models) are indicated by dashed vertical lines.

III.3.2 Landscape-dependence of crop diversity effects

The effect of CropDiv on BCI and predator densities was not influenced by SNH (no CropDiv x SNH interaction, Table III.1, Figures III.3b & III.3d). The only observed interaction relates to parasitoid densities at the most predictive 500 m scale (Table III.1). Here, the response to CropDiv changed from positive to negative with increasing landscape complexity.

III.3.3 Natural enemies and biological control

We found no relationship between BCI and the density of arthropod predators ($\sum w_i$ = 0.55, estimate (95% CIs) = -0.007 (-0.1, 0.08)) or parasitoids ($\sum w_i$ = 0.88, estimate = -0.02 (-0.07, 0.02)). Furthermore, the presence of birds did not affect overall biological control (Figure III.S1, Tables III.1 & III.S6) or aphid suppression by predators and parasitoids (bird exclusion x predator: $\sum w_i$ = 0.18, estimate = -0.006 (-0.116, 0.05), bird exclusion x parasitoid: $\sum w_i$ = 0.47, estimate = -0.003 (-0.139, 0.003).

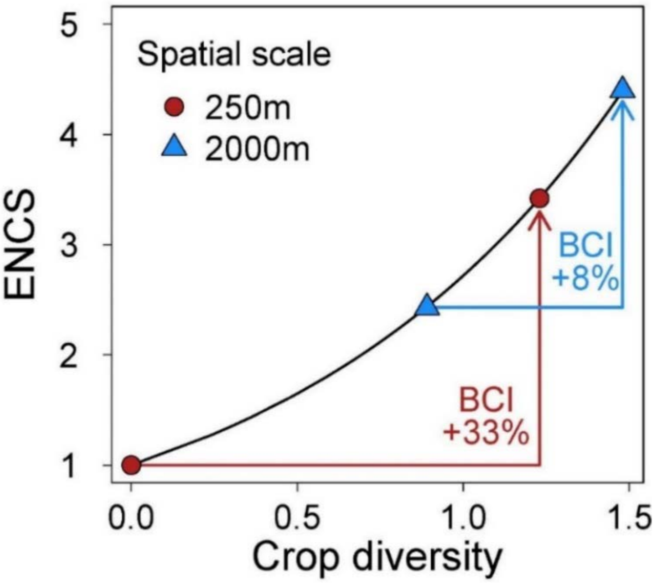


Figure III.4 Conversion of crop diversity (CropDiv) to 'effective number of crops' (ENCS, (Jost, 2006)). CropDiv was calculated as Shannon Wiener index based on 12 arable crop types (Table III.S1). Therefore, ENCS (exp (CropDiv)) indicates the number of equally abundant crop types required to achieve a specific CropDiv. In this graphic, crop diversification increases from the bottom left (low diversification) to the top right (high diversification). Benefits of crop diversification to BCI are shown for two spatial scales: on small scales (250m, circles), BCI increased by 33 %, on larger scales (2000m, triangles) by 8 %. Illustrated using minimum and maximum CropDiv/ENCS values (Table III.S1) and model-averaged estimates of BCI for the two most predictive scales (highest R^2 values of full models).

III.4 Discussion

Our study explored the scale- and landscape-specific influence of crop diversification on biological control of aphids in winter wheat. By disentangling the effects of landscape-level crop diversity and seminatural habitat cover (SNH) on six spatial scales, we demonstrate that crop diversity augments natural enemies and biological control (BCI). On small scales below 500 m, an increase from one to three dominating crop types enhanced BCI by up to 33 %. This contradicts previous studies linking biological control primarily to non-crop landscape composition and configuration rather than crop diversity (Holland *et al.*, 2012; Rusch *et al.*, 2013). However, our findings corroborate recent evidence for benefits of crop diversification on aphid suppression (Bosem Baillod *et al.*, 2017). Opposed to our predictions, arthropod predators and parasitoids did not differ greatly in the strength of their response to crop diversity and SNH. However, our findings suggest that natural enemies other than birds or the recorded arthropod predators and parasitoids were responsible for pest suppression in our system. This highlights the need to study the ecosystem service itself rather than individual natural enemy guilds.

III.4.1 Time and scale effects

We found delayed biological control most likely linked to the deferred arrival of predators, and higher attractiveness of treatment patches with increasing aphid densities (Chaplin-Kramer *et al.*, 2013; Martin *et al.*, 2016). Furthermore, the response of BCI to crop diversity switched from negative to positive during the course of the exclusion experiment. This suggests that initial dilution-concentration effects (Schneider *et al.*, 2015; Bosem Baillod *et al.*, 2017) were replaced by diversity- and abundance-mediated processes. Importantly, we show that the benefits of crop diversity would have gone unnoticed in experiments lasting less than ten days or restricted to a single spatial scale (e.g. 1000 m, commonly used in ecological studies). Crop diversity was most influential on small (<500m, biological control, predator densities) and large (>2000m, parasitoid densities) spatial scales, whereas SNH had no or weak effects across all scales.

To our knowledge, scale effects on overall biological control using comparable crop diversity indices and exclusion experiments have not previously been investigated. However, two recent studies report reduced aphid densities (1000 m scale; (Bosem Baillod *et al.*, 2017)) and increased levels of predation by epigeal predators (750m scale; (Holland *et al.*, 2012)) with crop diversification in similar cereal systems in Germany and the UK, respectively. These effects occurred on slightly larger scales than in our system. Yet scale-specific differences in the response to landscape variables are common, and depend on study region and system. For example, non-crop landscape complexity may influence overall or taxon-specific pest suppression and predator densities either at small (< 500 m; (Holland *et al.*, 2012; Tamburini *et al.*, 2015)), intermediate (> 500 m – 2000 m; (Gardiner *et al.*, 2009; Chaplin-Kramer *et al.*, 2013; Rusch *et al.*, 2013; Bosem Baillod *et al.*, 2017)) or large spatial scales (> 2000 m; (Gardiner *et al.*, 2009; Woltz *et al.*, 2012; Chaplin-Kramer *et al.*, 2013)). Due to their specialist diet and greater dispersal limitation, specialist parasitoids may be less responsive to resource diversification than generalist predators, and influenced more locally (Chaplin-Kramer *et al.*, 2011). Nevertheless, strong responses to large-scale landscape complexity were reported elsewhere, and compare well with our findings (1500 – 2000 m; e.g. (Thies *et al.*, 2003)).

III.4.2 Seminatural habitat and landscape interactions

Perennial non-crop structures are important sources of natural enemies in agroecosystems (Tscharntke *et al.*, 2005; Bosem Baillod *et al.*, 2017), and therefore have the potential to enhance pest regulation (Rusch *et al.*, 2016). Yet a growing evidence base suggests that natural habitat is not a panacea to improve biological control (Martin *et al.*, 2016; Tscharntke *et al.*, 2016). Some predators, especially those primarily relying on crop resources, benefit from non-crop removal, so that SNH enhancement might weaken overall biological control (Caballero-López *et al.*, 2012; Shackelford *et al.*, 2013). Alternatively, local habitat disturbance and pesticide intensity can override resource-related landscape complexity effects (Jonsson *et al.*, 2012). Natural habitat cover may also act as barrier to dispersal for natural enemies, lead to host/prey dilution or provide more favourable resources, thereby drawing natural enemies away from the crops (Holland *et al.*, 2012; Ratnadass *et al.*, 2012). This could explain the negative effect of SNH on parasitoid densities at the 500 m scale, especially in landscapes with a diversity of additional crop resources. In contrast, higher crop diversity in simple landscapes might sustain parasitoids by providing alternative hosts across the season, as seen here (Schellhorn *et al.*, 2015). Apart from this interaction between crop diversity and landscape complexity, we found no evidence for landscape-dependent effects of crop diversification (Woltz *et al.*, 2012; Rusch *et al.*, 2013).

III.4.3 Natural enemies and biological control

We expected natural enemy guilds to differ in their contribution to biological control, but this hypothesis was not confirmed. Surprisingly, we observed no correlations of biological control with the density of specialist parasitoids and (aerial) arthropod predators, although both groups were enhanced by crop diversification at different scales. These findings suggest that taxa not captured well with our sampling method, particularly epigeal Carabidae and Staphylinidae, or cryptic leaf-dwelling Chrysopidae, were primary drivers of pest suppression in our system. Epigeal predators can be important biocontrol agents (Martin *et al.*, 2013; Tamburini *et al.*, 2015) and contribute to increased predation in oilseed rape fields (Dainese *et al.*, 2017) and crop-diversified landscapes (Holland *et al.*, 2012). However, they are generally less mobile and more likely to depend on crop rather than non-crop resources (Shackelford *et al.*, 2013). Our results support this idea owing to strong small-scale effects of crop diversity on BCI, yet a lack of correlation with SNH at the same scales.

Our finding and previous research therefore highlights the importance of assessing overall biological control rather than the density of natural enemy guilds alone. Sampling deficits related to distinct guilds could mask influential correlations (Henri *et al.*, 2015). Moreover, species-specific predation and overall parasitism rates may not translate to high biological control owing to species interactions at the community level (Letourneau *et al.*, 2009; Woltz *et al.*, 2012; Shackelford *et al.*, 2013; Tamburini *et al.*, 2015). For example, insectivorous birds interfere with pest suppression by feeding on intermediate predators (Mooney *et al.*, 2010; Martin *et al.*, 2013). In our study, we did not observe reductions in overall biological control in the presence of birds (Tamburini *et al.*, 2015). However, the strength of intraguild predation by birds is known to vary strongly, depending on the system (temperate vs. tropical) or pest organism studied (e.g. chewing vs. sap-sucking insects; (Straub *et al.*, 2008)).

III.5 Synthesis and management implications

Agricultural landscapes are primarily crafted by market forces dictating farmers choices of what, where and how to produce (Bowman & Zilberman, 2013). Hence, the scope for implementing beneficial diversification practices is often limited. Societal, economic and bureaucratic obstacles deter conventional farmers from joining agri-environment schemes (state-subsidized wildlife conservation programs such as off-field flower plantings) or creating natural habitat in an attempt to extensify farming (e.g. by reducing insecticide applications, (Wilson & Tisdell, 2001; Lin, 2011)). Policy-based tools such as the inclusion of 'crop diversification' in the European Common Agricultural Policy ('Greening', EU Regulation No. 1307/2013) can favour positive changes. Nevertheless, potential 'Greening' benefits are probably lower than expected, as the minimum number of crops that needs to be grown is low (~ 3 crop species, (Pe'er *et al.*, 2014; Josefsson *et al.*, 2017)). Furthermore, the lacking requirement to cultivate functionally different crops could result in resource bottlenecks for natural enemies (Schellhorn *et al.*, 2015). Our study indicates that at least three functional crop groups (not crop species *per se*) ought to be cultivated to increase biological control. Hence, the conversion of crop diversity to 'effective number of crop types' (ENCS) can aid in the development of appropriate farm management guidelines that facilitate ecosystem services, and in the communication of research results to farmers and policy makers.

Although hypothesized links between crop diversity and yield, agrochemical usage, ecosystem resilience and farm economic stability need yet to be confirmed (Lin, 2011; Aguilar *et al.*, 2015), our study is one of the first to highlight the importance of crop diversity for biological control. From a farmer's perspective, landscape-level crop diversification for the sake of biological control is a promising alternative to on-field or non-crop diversification measures. Increasing the number of crop types on small landscape scales allows for a certain flexibility of implementation using extended crop rotation schemes and co-operation with neighbouring farms. Considering the adverse effects of agricultural intensification and climate change, this finding opens new potential pathways for the future of sustainable farming.

III.6 Supplement

III.6.1 Detailed description of experimental design and natural enemy exclusion experiment

III.6.1.1 Basic study design

This research was conducted as part of a larger field experiment within the framework of the project Liberation ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificATION"), funded by the European Union (grant number: 311781). This major study explored how local management practices (fertilizer application, insecticide input, field soil organic carbon) in combination with changes in cropland area at the expense of seminatural habitat determine the abundance of pests and predators, biological pest control, and crop yields. For this purpose, a common field experiment was designed and implemented in seven European countries participating in the research (Germany, Hungary, Italy, Poland, Sweden, The Netherlands, United Kingdom).

The common experiment incorporated a paired-field design (Figure III.1, main text), in which pairing was achieved by joining two conventional winter wheat fields of contrasting soil organic carbon content (= SOC, high/low) yet similar soil texture, pH (less than 0.5 unit difference) and field margin quality (mostly grassy edge) along a gradient of landscape simplification defined by the proportion of arable land in 1000m radius. In Germany, the 18 fields (nine field pairs, within-pair distance between fields mean±SE 1246±328, range 185-2496m) were also selected to cover landscapes with varying crop diversity at six spatial scales: 100, 250, 500, 1000, 2000 and 3000m (12 crop categories, Table III.S1, (Eurostat, 2012). Correlations between crop diversity and the amount of seminatural habitat, cropland cover, field size and overall habitat diversity on all spatial scales were kept to a minimum.

The paired design allowed to separate effects of increasing soil organic carbon from those of soil texture and pH. At the same time, fields were selected to include different management practices (e.g. till or no-till, long or short crop rotations, mineral vs. organic fertilizer input) to ensure that SOC effects were not in fact driven by specific field management types. Soil conditions of potential fields were assessed by collecting five soil cores (30mm diameter, 15cm deep). Samples were pooled within fields, homogenized and stored at 5°C before analyses of pH and SOC. In Germany, soil texture within potential fields was determined using soil maps (Bayerische Vermessungsverwaltung, 2010).

Study plots (> 50x15m) were established along the edge of each field, at least 15m from headlands. A crossed insecticide (pyrethroid insecticide, yes/no) and fertilizer treatment (no=0 kg/ha, yes= three applications of ammonium sulfate nitrate at ~BBCH 20 (90kg/ha), ~BBCH 30 (50kg/ha) and ~BBCH 55 (50kg/ha)) was established by randomly assigning each treatment combination to one of the four established subplots (12x14m each). Farmers were not allowed to use insecticides or fertilizers on or near study plots. Herbicides and fungicides were applied as usual. Natural enemy exclusion cages (see below) were only employed on non-insecticide plots, hence the treatment „insecticide“ is irrelevant for this study and therefore not shown in Figure III.1 (main text).

Owing to the underlying experimental design, we included both SOC and fertilization as covariates in our analysis. However, no effect on natural enemy abundances and SOC was observed (see Table III.1 main text, Figure III.S1). Additionally, preliminary analyses relating local field management to recorded aphid densities using a generalized mixed effects model with Poisson distribution did not reveal any effects of SOC ($\sum w_i$=0.36, estimate (95% confidence intervals)= -0.08 (-0.72, 0.3)) or Nitrogen ($\sum w_i$=0.29, estimate(CIs)= 0.01 (-0.3, 0.39)), nor their interaction ($\sum w_i$=0.03, estimate(CIs)= -0.006 (-0.81,0.49)).

III.6.1.2 Natural enemy exclusion experiment

During the grain milk stage (BBCH 66 to 77), aphid populations (3 populations per subplot = 6 populations per field, Figure III.1 in main text) were established on patches of winter wheat (30cm diameter, initial aphid density ~100), in which natural enemies had previously been removed manually and using pitfall traps. Patches were separated by at least 2m and covered with fiber web tents to prevent re-colonization of predators. We used lab-reared cereal aphids *Sitobion avenae* (Katz Biotech AG) that had been acclimated to local conditions for 14 days prior to establishment. Establishment success was monitored after five days, and patches were re-inoculated if necessary. Day 10 after the first inoculation marked the starting date of the natural enemy exclusion experiment. Three exclusion treatments were set up: 'Open Treatment' (access for flying and ground-dwelling arthropods, birds and parasitoids), 'Bird Exclosure' (only bird predators excluded) and 'Full Exclosure' (=control all birds, arthropod predators and parasitoids excluded) (Figure III.1, main text). Due to variable establishment success, care was taken to achieve similar starting densities for aphids across all treatments (mean$\pm$SE aphid densities 'Bird Exclosure' 86.44$\pm$17.47, 'Full Exclosure' 94.33$\pm$19.61, 'Open treatment' 126.19$\pm$30.73, Figure III.S1). Exclusion cages consisted of 30x100cm plastic mesh cylinders ('Bird Exclosure' mesh size 20x20mm, 'Full Exclosure' mesh size 5x5mm). Additionally, 'Full Exclosure' cages were covered in sticky glue (Thies *et al.*, 2011), and metal rings (32cm diameter, 25cm high) were inserted 10cm into the ground to prevent re-colonization of flying and ground-dwelling predators. In total, each field received two replicates per exclusion treatment (6 cages per field), one per fertilization subplot (fertilized *vs.* non-fertilized; Figure III.1).

Within each exclusion treatment, aphids were counted non-destructively on 10 randomly selected tillers in 5-day intervals (day 0, 5, 10, 15). Additionally, we recorded the number of aphid mummies and natural predators such as vegetation-dwelling hoverfly, ladybird and lacewing larvae and spiders, and aerial predators such as adult ladybirds and parasitoids in order to investigate effects on predator density and parasitism rate. The strength of biological control for each five-day interval was assessed by calculating a biological control index (BCI, (Gardiner *et al.*, 2009) for the treatments 'Bird Exclosure' and 'Open treatment' as

$$Biological\ control\ index = 1 - \frac{A_{treatment_{end}}}{r_{full\ exclosure} * A_{treatment_{start}}}$$

where $A_{treatment\ end}$ is the number of aphids in the treatment on the final day, $r_{full\ exclosure}$ is the ratio of final to initial aphid numbers in the 'Full exclosure' (aphid population growth when all predators are excluded), and $A_{treatment\ start}$ is the initial number of aphids in the treatment. The BCI metric ranges from 0 (no net reduction in aphid densities in open treatments) to 1 (optimal biological control, 100% of aphids consumed). Following (Gardiner *et al.*, 2009) negative BCI values were set to zero as these indicate ineffective biological control. BCI was calculated separately for 'Bird exclosure' and 'Open treatments' for three 5-day intervals ('BCI', days 0 to 5, 5 to 10, 10 to 15). Predator densities were pooled across all predatory guilds for each sampling round (days 5, 10, 15). Due to the low rate of parasitism, analysis of parasitism rate (the fraction of parasitized to total aphids) was restricted to day 15.

Table III.S1 Summary statistics of landscape parameters used in analyses (crop diversity and proportion of seminatural habitat) for each of the six landscape scales (18 fields). For crop diversity, the minimum and maximum effective number of crop species (ENCS) was calculated as exp(crop diversity) (Jost, 2006).

Scale	*N*	Mean	SD	SE	Min	ENCS Min	Max	ENCS Max	Description
Crop diversity									
100	18	0.58	0.37	0.09	0.00	1.00	1.32	3.72	Shannon index calculated from the proportional cover of twelve crop types: cereals (excluding grain maize), 1- or 2-year old fallows, flowers and ornamental plants, temporary grassland and green fodder (green maize), legumes, maize, oilseed and fiber crops (excluding rape), rape and turnips, root crops, sunflowers, vegetables, other industrial crops (Eurostat, 2012)
250	18	0.66	0.32	0.08	0.00*	1.00*	1.24*	3.45*	
500	18	0.90	0.26	0.06	0.50	1.65	1.44	4.23	
1000	18	1.06	0.23	0.06	0.74	2.10	1.44	4.23	
2000	18	1.21	0.19	0.04	0.89*	2.44*	1.48*	4.41*	
3000	18	1.24	0.14	0.03	1.03	2.79	1.47	4.34	
Seminatural habitat cover									
100	18	24.95	24.77	5.84	2.19	-	76.88	-	Proportional cover (%) of natural habitats including extensive perennial grassland, orchard meadows, hedgerows, forest edges (10 m into the forest), field and grass margins along linear elements (rivers and roads)
250	18	26.47	23.20	5.47	1.16	-	76.55	-	
500	18	24.91	16.08	3.79	4.51	-	53.00	-	
1000	18	24.15	13.57	3.20	8.35	-	53.50	-	
2000	18	21.95	10.45	2.46	7.98	-	40.66	-	
3000	18	21.28	8.60	2.03	10.08	-	36.98	-	

Table III.S2 Correlation matrix (Pearson's r) of predictor and landscape variables for each spatial scale (100m, 250m, 500m, 1000m, 2000m, 3000m). Landscape-level crop diversity (CropDiv) is the Shannon Wiener index of 12 arable crop categories. SNH = seminatural habitat cover, HabDiv = landscape-level habitat diversity based on the Shannon Wiener index of 6 broadly classified land use types in the study area (annual crops, perennial crops, seminatural habitat, forest, water, urban), SOC = soil organic carbon content (low, high), Fertilization (yes, no), Aphids= aphid densities recorded within each treatment. Values above and below diagonals report correlations at successive spatial scales.

	CropDiv	% SNH	% Arable	HabDiv	Field size	Aphids	Fertilization*	SOC*	
CropDiv	-	0.026	0.054	0.41	0.48	0.23	0	0.28	
% SNH	0.22	-	0.99	0.65	0.55	0.11	0	0.18	
% Arable	0.092	0.95	-	0.74	0.6	0.11	0	0.21	
HabDiv	0.27	0.56	0.74	-	0.66	0.14	0	0.3	
Field size	0.51	0.36	0.42	0.43	-	0.21	0	0.16	**100m**
Aphids	0.13	0.11	0.1	0.14	0.046	-	0	0.14	
Fertilization*	0	0	0	0	0	0	-	0	
SOC*	0.044	0.12	0.17	0.023	0.012	0.14	0	-	
				250m					
CropDiv	-	0.28	0.21	0.018	0.47	0.082	0	0.2	
% SNH	0.47	-	0.92	0.8	0.11	0.16	0	0.057	
% Arable	0.34	0.9	-	0.93	0.23	0.12	0	0.042	
HabDiv	0.17	0.77	0.94	-	0.4	0.09	0	0.003	**500m**
Field size	0.17	0.24	0.4	0.56	-	0.02	0	0.022	
Aphids	0.018	0.24	0.16	0.13	0.032	-	0	0.14	
Fertilization*	0	0	0	0	0	0	-	0	
SOC*	0.24	0.14	0.051	0.12	0.046	0.14	0	-	
				1000m					
CropDiv	-	0.33	0.022	0.07	0.067	0.16	0	0.16	
% SNH	0.25	-	0.87	0.81	0.34	0.22	0	0.074	
% Arable	0.11	0.86	-	0.97	0.44	0.12	0	0.032	
HabDiv	0.12	0.82	0.95	-	0.6	0.12	0	0.028	**2000m**
Field size	0.2	0.4	0.63	0.72	-	0.015	0	0.096	
Aphids	0.12	0.22	0.12	0.1	0.04	-	0	0.14	
Fertilization*	0	0	0	0	0	0	-	0	
SOC*	0.13	0.049	0.001	0.037	0.13	0.14	0	-	
				3000m					

* Fertilization (fertilization treatment yes/no) and SOC (soil organic carbon content low/high) are shown due to the nature of the experimental design and analysis, yet not further developed in this paper (see Methods).

Table III.S3 Full landscape models (general or generalized linear mixed effects models) for biological control, predator density and parasitism rate. Separate models were built for each of the six landscape scales around study fields (100m, 250m, 500m, 1000m, 2000m, 3000m). The random effect structure accounted for the nested design: fields within a pair (‘Pair’), two fertilization treatment levels per field (‘Field’), three exclusion treatments in every fertilization subplot (‘Subplot’). For predator density the random term ‘Cage’ accounted for replication within each exclusion treatment (three predator and aphid surveys). Model fit of full models was assessed with marginal (R^2m) and conditional (R^2c) R-squared for every landscape scale, and average R^2 values (± SE) were calculated across scales.

Response variable					
Scale	Distribution	Fixed effects*	Random effects	R^2m	R^2c
Biological control					
100m	normal	F + SOC + B + S + CropDiv + SNH + CropDiv:S + CropDiv:SNH	Pair/Field/Subplot/Cage	0.22	0.27
250m				0.23	0.28
500m				0.22	0.26
1000m				0.2	0.23
2000m				0.19	0.22
3000m				0.21	0.23
Mean R^2(±SE)				0.21 (±0.005)	0.25 (±0.009)
Predator density					
100m	Poisson	A + F + SOC + B + S + CropDiv + SNH + CropDiv:S CropDiv:SNH	Pair/Field/Subplot/Cage	0.27	0.30
250m				0.27	0.30
500m				0.23	0.29
1000m				0.20	0.30
2000m				0.21	0.31
3000m				0.21	0.30
Mean R^2(±SE)				0.23 (±0.01)	0.30 (±0.002)
Parasitoid density†					
100m	Poisson	A + F + SOC + B + CropDiv + SNH + CropDiv:SNH	Pair/Field/Subplot	0.23	0.4
250m				0.26	0.36
500m				0.43	0.47
1000m				0.26	0.39
2000m				0.35	0.43
3000m				0.29	0.38
Mean R^2(±SE)				0.3 (±0.03)	0.41 (±0.01)

* Fixed effects abbreviations: A = Aphid density, B = Bird exclusion (birds excluded yes/no), CropDiv = Crop diversity, F = Nitrogen fertilization (fertilizer applied yes/no), SNH = Proportion of seminatural habitat, SOC = Soil organic carbon content (soil organic carbon content low/high), S = Survey interval (days 0 to 5, 5 to 10 and 10 to 15), CropDiv:S = Interaction Crop diversity x Survey interval, CropDiv:SNH= Interaction Crop diversity x Proportion of seminatural habitat. Fertilization and SOC are included due to the nature of the experimental design and analysis, yet not further developed in this paper

† Parasitoid density was only analyzed for day 15, as parasitoid density was very low on days 5 and 10. No temporal effect was tested thus a random effect for Cage was not included.

Table III.S4 Full models (general linear mixed effects models) relating bird predation, predator and parasitoid densities to biological control. Model fit of full models was assessed with marginal (R^2m) and conditional (R^2c) R-squared. The random effect structure accounted for the nested design: fields within a pair ('Pair'), two fertilization treatment levels per field ('Field'), three exclusion treatments in every fertilization subplot ('Subplot'). For predator density the random term 'Cage' accounted for replication within each exclusion treatment (three predator and aphid surveys).

Response variable	Model distribution	Fixed effects*	Random effects	R^2m	R^2c
Biological control	normal	B+ S + PR + PR:S + PR:B + B:S:PR	Pair/Field/Subplot/Cage	0.2	0.23
Biological control	normal	B + PA + PA+B	Pair/Field/Subplot	0.13	0.42

* Fixed effects abbreviations: B = Bird exclusion (birds excluded yes/no), PR = predator density, PA = parasitoid density, S = Survey interval (days 0 to 5, 5 to 10 and 10 to 15).

† Effect of parasitoid density on biological control was only analyzed for day 15, as parasitoid density was very low on days 5 and 10. No temporal effect was tested thus a random effect for Cage was not included.

Table III.S5 Estimates and model weights of landscape models with ΔAICc < 7 for six spatial scales (100m, 250m, 500m, 1000m, 2000m and 3000m) for biological control, predator and parasitoid density. Models are listed in descending order according to their ΔAICc. Standardized parameter estimates, degrees of freedom (df), Akaike's Information Criterion with small-sample size adjustment (AICc), ΔAICc, Akaike weights (w_i) of each explanatory variable for the set of top models and summed weights ($\sum w_i$) for each scale based on model averaging are reported. Model fit was assessed using marginal (R^2m) and conditional (R^2c) R-squared values for each top model. '+' indicates the inclusion of the categorical variable in the specific top model, 'NA' parameters not selected in set of top models, and '-' parameters not used in full model. $\sum w_i$ with 95% confidence intervals of estimates excluding zero are highlighted in bold.

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R^2m	R^2c
Biological control (BCI)																	
100																	
	0.408	-0.056		+	+			-	+		15	-44.7	121.7	0.0	0.19	0.22	0.28
	0.378	-0.056		+				-	+		14	-45.9	121.8	0.1	0.18	0.21	0.27
	0.389	-0.046		+	+		+	-	+		16	-44.4	123.6	1.8	0.07	0.22	0.28
	0.378	-0.056	-0.018	+				-	+		15	-45.6	123.6	1.9	0.07	0.21	0.26
	0.424	-0.056		+	+	+		-	+		16	-44.4	123.6	1.9	0.07	0.22	0.28
	0.358	-0.045		+			+	-	+		15	-45.6	123.6	1.9	0.07	0.21	0.26
	0.394	-0.056		+		+		-	+		15	-45.6	123.6	1.9	0.07	0.21	0.26
	0.394	-0.056	-0.019	+		+		-	+		16	-45.4	125.4	3.7	0.03	0.21	0.26
	0.424	-0.057	-0.018	+	+	+		-	+		17	-44.2	125.4	3.7	0.03	0.22	0.28
	0.374	-0.045		+		+	+	-	+		16	-45.4	125.5	3.7	0.03	0.21	0.26
	0.404	-0.046		+	+	+	+	-	+		17	-44.2	125.5	3.8	0.03	0.22	0.27
	0.393	-0.049	-0.015	+	+		+	-	+		17	-44.3	125.6	3.9	0.03	0.22	0.28
	0.362	-0.048	-0.015	+			+	-	+		16	-45.5	125.6	3.9	0.03	0.21	0.26
	0.408	-0.057	-0.019	+	+			-	+	-0.002	17	-44.4	125.9	4.2	0.02	0.22	0.28
	0.378	-0.056	-0.019	+				-	+	-0.002	16	-45.6	125.9	4.2	0.02	0.21	0.26
	0.378	-0.048	-0.015	+		+	+	-	+		17	-45.2	127.5	5.8	0.01	0.21	0.26
	0.408	-0.049	-0.015	+	+	+	+	-	+		18	-44.0	127.5	5.8	0.01	0.22	0.27
	0.394	-0.056	-0.019	+		+		-	+	-0.002	17	-45.4	127.8	6.1	0.01	0.21	0.26
	0.424	-0.057	-0.019	+	+	+		-	+	-0.002	18	-44.2	127.8	6.1	0.01	0.22	0.28
	0.393	-0.049	-0.014	+	+		+	-	+	0.001	18	-44.3	128.0	6.3	0.01	0.22	0.28
	0.362	-0.048	-0.014	+			+	-	+	0.001	17	-45.5	128.0	6.3	0.01	0.21	0.26

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	$\sum w_i$	**(1)**	0.29	**(1)**	0.47	0.3	0.3	-	**0.99**	0.09							
250																	
	0.380	-0.102		+				-	+		14	-44.7	119.5	0.0	0.22	0.21	0.26
	0.407	-0.101		+	+			-	+		15	-43.8	120.0	0.5	0.17	0.22	0.27
	0.392	-0.101		+		+		-	+		15	-44.6	121.6	2.0	0.08	0.21	0.26
	0.380	-0.107	-0.012	+				-	+		15	-44.6	121.7	2.1	0.07	0.21	0.26
	0.390	-0.102		+			+	-	+		15	-44.7	121.7	2.2	0.07	0.21	0.26
	0.418	-0.101		+	+	+		-	+		16	-43.7	122.1	2.5	0.06	0.22	0.27
	0.417	-0.101		+	+		+	-	+		16	-43.7	122.2	2.6	0.06	0.22	0.27
	0.407	-0.106	-0.011	+	+			-	+		16	-43.7	122.2	2.6	0.06	0.22	0.27
	0.392	-0.107	-0.012	+		+		-	+		16	-44.5	123.7	4.2	0.03	0.21	0.26
	0.401	-0.101		+		+	+	-	+		16	-44.5	123.8	4.2	0.03	0.21	0.26
	0.391	-0.107	-0.013	+			+	-	+		16	-44.6	123.8	4.3	0.03	0.21	0.26
	0.381	-0.106	-0.010	+				-	+	0.004	16	-44.6	124.0	4.5	0.02	0.21	0.26
	0.428	-0.101		+	+	+	+	-	+		17	-43.6	124.3	4.7	0.02	0.22	0.27
	0.418	-0.105	-0.011	+	+	+		-	+		17	-43.6	124.3	4.7	0.02	0.22	0.27
	0.418	-0.106	-0.012	+	+		+	-	+		17	-43.6	124.4	4.8	0.02	0.22	0.27
	0.407	-0.105	-0.009	+	+			-	+	0.004	17	-43.7	124.5	5.0	0.02	0.22	0.27
	0.402	-0.107	-0.013	+		+	+	-	+		17	-44.4	125.9	6.4	0.01	0.21	0.26
	0.393	-0.106	-0.010	+		+		-	+	0.005	17	-44.5	126.1	6.5	0.01	0.21	0.26
	0.395	-0.105	-0.008	+			+	-	+	0.011	17	-44.5	126.1	6.6	0.01	0.21	0.26
	0.429	-0.106	-0.012	+	+	+	+	-	+		18	-43.5	126.5	6.9	0.01	0.22	0.27
	$\sum w_i$	**(1)**	0.31	**(1)**	0.44	0.26	0.25	-	**1**	0.07							
500																	
	0.378	-0.098		+				-	+		14	-47.7	125.6	0.0	0.16	0.20	0.25
	0.408	-0.099		+	+			-	+		15	-46.6	125.7	0.1	0.15	0.21	0.27
	0.394	-0.098		+		+		-	+		15	-47.5	127.4	1.8	0.06	0.20	0.25
	0.396	-0.102	0.001	+				-	+	0.065	16	-46.4	127.4	1.9	0.06	0.21	0.24
	0.424	-0.099		+	+	+		-	+		16	-46.4	127.5	2.0	0.06	0.21	0.26
	0.378	-0.101	-0.012	+				-	+		15	-47.6	127.7	2.1	0.06	0.20	0.25

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	0.425	-0.102	0.002	+	+			-	+	0.064	17	-45.3	127.7	2.1	0.06	0.22	0.26
	0.388	-0.100		+			+	-	+		15	-47.7	127.7	2.2	0.05	0.20	0.25
	0.408	-0.102	-0.012	+	+			-	+		16	-46.5	127.8	2.3	0.05	0.21	0.26
	0.419	-0.100		+	+		+	-	+		16	-46.6	127.8	2.3	0.05	0.21	0.27
	0.412	-0.102	0.001	+		+		-	+	0.065	17	-46.1	129.3	3.7	0.02	0.21	0.24
	0.394	-0.102	-0.012	+		+		-	+		16	-47.4	129.5	4.0	0.02	0.20	0.25
	0.442	-0.102	0.002	+	+	+		-	+	0.064	18	-45.0	129.5	4.0	0.02	0.22	0.26
	0.403	-0.100		+		+	+	-	+		16	-47.4	129.6	4.0	0.02	0.20	0.25
	0.406	-0.104	-0.0001	+			+	-	+	0.064	17	-46.3	129.6	4.1	0.02	0.21	0.25
	0.424	-0.102	-0.012	+	+	+		-	+		17	-46.3	129.7	4.1	0.02	0.21	0.26
	0.434	-0.100		+	+	+	+	-	+		17	-46.3	129.7	4.2	0.02	0.21	0.27
	0.390	-0.104	-0.013	+			+	-	+		16	-47.5	129.8	4.3	0.02	0.20	0.25
	0.435	-0.104	0.000	+	+		+	-	+	0.063	18	-45.2	129.9	4.4	0.02	0.22	0.26
	0.420	-0.104	-0.013	+	+		+	-	+		17	-46.4	130.0	4.4	0.02	0.21	0.27
	0.421	-0.104	-0.0001	+		+	+	-	+	0.065	18	-46.0	131.5	6.0	0.01	0.21	0.25
	0.405	-0.104	-0.013	+		+	+	-	+		17	-47.3	131.7	6.1	0.01	0.20	0.25
	0.451	-0.104	0.0004	+	+	+	+	-	+	0.064	19	-45.0	131.8	6.2	0.01	0.22	0.26
	0.435	-0.105	-0.013	+	+	+	+	-	+		18	-46.2	131.9	6.3	0.01	0.21	0.27
	$\sum w_i$	**(1)**	0.42	**(1)**	0.48	0.28	0.25	-	**1**	0.22							
1000																	
	0.378	-0.116	-0.044	+				-	+		15	-50.0	132.3	0.0	0.11	0.18	0.21
	0.378	-0.095		+				-	+		14	-51.1	132.4	0.0	0.11	0.18	0.22
	0.407	-0.095		+	+			-	+		15	-50.1	132.6	0.3	0.10	0.19	0.24
	0.407	-0.115	-0.043	+	+			-	+		16	-49.0	132.8	0.4	0.09	0.19	0.23
	0.401	-0.124	-0.051	+			+	-	+		16	-49.5	133.8	1.5	0.05	0.19	0.22
	0.394	-0.116	-0.045	+		+		-	+		16	-49.7	134.2	1.8	0.05	0.19	0.21
	0.430	-0.124	-0.050	+	+		+	-	+		17	-48.6	134.2	1.9	0.04	0.20	0.23
	0.393	-0.095		+		+		-	+		15	-50.9	134.2	1.9	0.04	0.18	0.22
	0.391	-0.098		+			+	-	+		15	-51.0	134.5	2.1	0.04	0.18	0.23
	0.422	-0.095		+	+	+		-	+		16	-49.9	134.5	2.2	0.04	0.19	0.24
	0.422	-0.116	-0.044	+	+	+		-	+		17	-48.8	134.6	2.3	0.04	0.19	0.23

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	0.375	-0.119	-0.048	+				-	+	-0.006	16	-50.0	134.7	2.3	0.04	0.18	0.21
	0.421	-0.098		+	+		+	-	+		16	-50.0	134.7	2.4	0.03	0.19	0.24
	0.404	-0.118	-0.047	+	+			-	+	-0.006	17	-49.0	135.1	2.7	0.03	0.19	0.23
	0.417	-0.124	-0.051	+		+	+	-	+		17	-49.3	135.7	3.3	0.02	0.19	0.22
	0.397	-0.129	-0.057	+			+	-	+	-0.012	17	-49.5	136.1	3.7	0.02	0.19	0.22
	0.446	-0.124	-0.051	+	+	+	+	-	+		18	-48.3	136.1	3.8	0.02	0.20	0.23
	0.406	-0.098		+		+	+	-	+		16	-50.8	136.4	4.0	0.02	0.18	0.23
	0.391	-0.119	-0.048	+		+		-	+	-0.007	17	-49.7	136.5	4.2	0.01	0.19	0.21
	0.426	-0.129	-0.057	+	+		+	-	+	-0.012	18	-48.5	136.5	4.2	0.01	0.20	0.23
	0.435	-0.098		+	+	+	+	-	+		17	-49.8	136.7	4.3	0.01	0.19	0.24
	0.419	-0.119	-0.047	+	+	+		-	+	-0.007	18	-48.8	137.0	4.6	0.01	0.19	0.23
	0.367			+				-			11	-56.9	137.0	4.7	0.01	0.15	0.20
	0.400			+	+			-			12	-55.8	137.1	4.8	0.01	0.16	0.21
	0.413	-0.130	-0.058	+		+	+	-	+	-0.012	18	-49.2	138.0	5.6	0.01	0.19	0.22
	0.367		-0.029	+				-			12	-56.2	138.0	5.6	0.01	0.16	0.20
	0.399		-0.029	+	+			-			13	-55.1	138.1	5.8	0.01	0.17	0.21
	0.442	-0.130	-0.057	+	+	+	+	-	+	-0.012	19	-48.3	138.4	6.1	0.01	0.20	0.23
	0.383			+		+		-			12	-56.7	138.9	6.5	0.00	0.15	0.20
	0.415			+	+	+		-			13	-55.6	139.0	6.7	0.00	0.16	0.21
	0.380			+			+	-			12	-56.8	139.0	6.7	0.00	0.15	0.20
	0.414			+	+		+	-			13	-55.7	139.1	6.8	0.00	0.16	0.22
	0.368	-0.004		+				-			12	-56.9	139.3	6.9	0.00	0.15	0.20
	$\sum w_i$	**(0.94)**	0.57	**(1)**	0.46	0.28	0.3	-	**0.91**	0.13							
2000																	
	0.379	-0.108	-0.045	+				-	+		15	-50.9	134.1	0.0	0.10	0.18	0.21
	0.405	-0.107	-0.045	+	+			-	+		16	-50.0	134.8	0.7	0.07	0.19	0.22
	0.379	-0.093		+				-	+		14	-52.4	134.9	0.8	0.06	0.17	0.22
	0.406	-0.092		+	+			-	+		15	-51.6	135.5	1.4	0.05	0.18	0.23
	0.396	-0.108	-0.046	+		+		-	+		16	-50.6	135.9	1.7	0.04	0.18	0.21
	0.397	-0.112	-0.048	+			+	-	+		16	-50.6	135.9	1.8	0.04	0.19	0.22
	0.367			+				-			11	-56.5	136.3	2.1	0.03	0.15	0.20

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	0.376	-0.108	-0.046	+				-	+	-0.008	16	-50.8	136.3	2.2	0.03	0.18	0.21
	0.424	-0.111	-0.048	+	+		+	-	+		17	-49.7	136.5	2.4	0.03	0.19	0.23
	0.397			+	+			-			12	-55.5	136.6	2.5	0.03	0.16	0.22
	0.422	-0.107	-0.045	+	+	+		-	+		17	-49.8	136.6	2.5	0.03	0.19	0.22
	0.396	-0.093		+		+		-	+		15	-52.1	136.7	2.6	0.03	0.17	0.21
	0.365		-0.034	+				-			12	-55.6	136.7	2.6	0.03	0.16	0.20
	0.392	-0.095		+			+	-	+		15	-52.3	137.0	2.9	0.02	0.17	0.22
	0.403	-0.107	-0.046	+	+			-	+	-0.008	17	-50.0	137.0	2.9	0.02	0.19	0.22
	0.396		-0.034	+	+			-			13	-54.6	137.1	2.9	0.02	0.17	0.22
	0.367	-0.034	-0.045	+				-			13	-54.7	137.3	3.1	0.02	0.17	0.20
	0.422	-0.092		+	+	+		-	+		16	-51.3	137.3	3.2	0.02	0.18	0.22
	0.420	-0.094		+	+		+	-	+		16	-51.4	137.6	3.4	0.02	0.18	0.23
	0.414	-0.112	-0.048	+		+	+	-	+		17	-50.3	137.7	3.5	0.02	0.19	0.21
	0.396	-0.033	-0.045	+	+			-			14	-53.9	137.8	3.7	0.02	0.18	0.21
	0.383			+		+		-			12	-56.2	138.0	3.9	0.01	0.15	0.20
	0.368	-0.019		+				-			12	-56.2	138.0	3.9	0.01	0.16	0.20
	0.394	-0.108	-0.046	+		+		-	+	-0.008	17	-50.5	138.1	4.0	0.01	0.18	0.21
	0.394	-0.112	-0.048	+			+	-	+	-0.008	17	-50.5	138.1	4.0	0.01	0.19	0.22
	0.378			+			+	-			12	-56.4	138.3	4.2	0.01	0.16	0.21
	0.441	-0.111	-0.048	+	+	+	+	-	+		18	-49.5	138.4	4.3	0.01	0.20	0.22
	0.413			+	+	+		-			13	-55.3	138.4	4.3	0.01	0.16	0.21
	0.398	-0.017		+	+			-			13	-55.3	138.4	4.3	0.01	0.16	0.21
	0.381		-0.034	+		+		-			13	-55.3	138.5	4.4	0.01	0.16	0.20
	0.411			+	+		+	-			13	-55.4	138.6	4.5	0.01	0.16	0.22
	0.379		-0.035	+			+	-			13	-55.4	138.7	4.5	0.01	0.17	0.21
	0.409	-0.095		+		+	+	-	+		16	-52.0	138.8	4.6	0.01	0.17	0.22
	0.422	-0.111	-0.048	+	+		+	-	+	-0.007	18	-49.7	138.8	4.7	0.01	0.19	0.23
	0.419	-0.107	-0.046	+	+	+		-	+	-0.008	18	-49.7	138.9	4.7	0.01	0.19	0.22
	0.387	-0.038	-0.048	+			+	-			14	-54.4	138.9	4.8	0.01	0.18	0.20
	0.411		-0.034	+	+	+		-			14	-54.4	138.9	4.8	0.01	0.17	0.21
	0.411		-0.035	+	+		+	-			14	-54.4	139.0	4.8	0.01	0.17	0.22
	0.384	-0.035	-0.045	+		+		-			14	-54.5	139.0	4.9	0.01	0.17	0.19

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	0.418	-0.037	-0.047	+	+		+	-			15	-53.5	139.4	5.3	0.01	0.18	0.21
	0.436	-0.094		+	+	+	+	-	+		17	-51.2	139.4	5.3	0.01	0.18	0.23
	0.364	-0.034	-0.046	+				-		-0.008	14	-54.7	139.4	5.3	0.01	0.17	0.20
	0.413	-0.033	-0.045	+	+	+		-			15	-53.6	139.6	5.5	0.01	0.18	0.20
	0.385	-0.019		+		+		-			13	-56.0	139.7	5.6	0.01	0.16	0.20
	0.411	-0.112	-0.048	+		+	+	-	+	-0.007	18	-50.2	139.9	5.8	0.01	0.19	0.21
	0.383	-0.021		+			+	-			13	-56.1	140.0	5.8	0.01	0.16	0.20
	0.393	-0.032	-0.045	+	+			-		-0.008	15	-53.8	140.0	5.9	0.01	0.18	0.21
	0.394			+		+	+	-			13	-56.1	140.1	5.9	0.00	0.16	0.21
	0.414	-0.018		+	+	+		-			14	-55.1	140.2	6.1	0.00	0.16	0.21
	0.414	-0.019		+	+		+	-			14	-55.1	140.4	6.2	0.00	0.17	0.22
	0.426			+	+	+	+	-			14	-55.2	140.5	6.3	0.00	0.16	0.22
	0.394		-0.035	+		+	+	-			14	-55.2	140.5	6.4	0.00	0.17	0.21
	0.404	-0.039	-0.048	+		+	+	-			15	-54.1	140.7	6.5	0.00	0.18	0.20
	0.438	-0.111	-0.048	+	+	+	+	-	+	-0.007	19	-49.4	140.7	6.5	0.00	0.20	0.22
	0.426		-0.035	+	+	+	+	-			15	-54.2	140.9	6.7	0.00	0.18	0.22
	0.384	-0.037	-0.048	+			+	-		-0.007	15	-54.3	141.1	7.0	0.00	0.18	0.20
	$\sum w_i$	**(0.79)**	0.62	**(1)**	0.43	0.29	0.28	-	**0.65**	0.13							
3000																	
	0.378	-0.123		+				-	+		14	-49.9	129.9	0.0	0.11	0.18	0.23
	0.407	-0.123		+	+			-	+		15	-48.9	130.2	0.4	0.09	0.19	0.24
	0.378	-0.131	-0.034	+				-	+		15	-49.0	130.4	0.5	0.09	0.19	0.22
	0.368	-0.140	-0.037	+				-	+	-0.042	16	-47.9	130.6	0.7	0.08	0.20	0.22
	0.406	-0.131	-0.033	+	+			-	+		16	-48.1	130.8	1.0	0.07	0.20	0.23
	0.395	-0.140	-0.037	+	+			-	+	-0.042	17	-47.0	131.1	1.2	0.06	0.20	0.23
	0.397	-0.123		+		+		-	+		15	-49.5	131.4	1.6	0.05	0.18	0.22
	0.425	-0.123		+	+	+		-	+		16	-48.6	131.9	2.0	0.04	0.19	0.23
	0.391	-0.124		+			+	-	+		15	-49.8	131.9	2.1	0.04	0.19	0.23
	0.397	-0.131	-0.034	+		+		-	+		16	-48.6	132.0	2.1	0.04	0.19	0.22
	0.387	-0.140	-0.037	+		+		-	+	-0.042	17	-47.5	132.2	2.3	0.04	0.20	0.22
	0.421	-0.124		+	+		+	-	+		16	-48.8	132.3	2.4	0.03	0.19	0.24

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	0.393	-0.133	-0.035	+			+	-	+		16	-48.8	132.3	2.5	0.03	0.19	0.23
	0.384	-0.143	-0.038	+			+	-	+	-0.043	17	-47.7	132.4	2.5	0.03	0.20	0.22
	0.424	-0.131	-0.033	+	+	+		-	+		17	-47.7	132.5	2.6	0.03	0.20	0.23
	0.414	-0.140	-0.037	+	+	+		-	+	-0.042	18	-46.6	132.7	2.9	0.03	0.21	0.23
	0.422	-0.133	-0.035	+	+		+	-	+		17	-47.8	132.8	2.9	0.03	0.20	0.24
	0.412	-0.142	-0.038	+	+		+	-	+	-0.043	18	-46.7	132.9	3.0	0.02	0.21	0.23
	0.409	-0.124		+		+	+	-	+		16	-49.4	133.5	3.7	0.02	0.19	0.23
	0.438	-0.124		+	+	+	+	-	+		17	-48.4	134.0	4.1	0.01	0.20	0.24
	0.411	-0.133	-0.035	+		+	+	-	+		17	-48.4	134.0	4.1	0.01	0.20	0.22
	0.402	-0.142	-0.038	+		+	+	-	+	-0.043	18	-47.3	134.0	4.2	0.01	0.20	0.22
	0.440	-0.133	-0.035	+	+	+	+	-	+		18	-47.5	134.5	4.6	0.01	0.20	0.23
	0.430	-0.142	-0.038	+	+	+	+	-	+	-0.043	19	-46.4	134.6	4.7	0.01	0.21	0.23
	$\sum w_i$	**(0.98)**	0.59	**(1)**	0.44	0.31	0.27	-	**0.97**	0.28							
Predator density																	
100																	
	-0.576	0.276	0.155	+			+	0.253	+		13	-316.3	660.5	0.0	0.15	0.27	0.29
	-0.527	0.242		+			+	0.258	+		12	-317.8	661.0	0.6	0.11	0.25	0.28
	-0.596	0.320	0.153	+			+	0.257			11	-319.2	661.7	1.3	0.08	0.27	0.29
	-0.623	0.286	0.157	+	+		+	0.241	+		14	-316.0	662.1	1.6	0.07	0.28	0.30
	-0.550	0.290		+			+	0.262			10	-320.6	662.3	1.8	0.06	0.25	0.27
	-0.556	0.273	0.154	+		+	+	0.255	+		14	-316.3	662.6	2.2	0.05	0.27	0.29
	-0.573	0.251		+	+		+	0.246	+		13	-317.4	662.6	2.2	0.05	0.25	0.28
	-0.569	0.276	0.148	+			+	0.251	+	-0.017	14	-316.3	662.7	2.2	0.05	0.28	0.29
	-0.505	0.238		+		+	+	0.260	+		13	-317.7	663.1	2.7	0.04	0.25	0.28
	-0.644	0.322	0.155	+	+		+	0.246			12	-318.8	663.2	2.7	0.04	0.27	0.29
	-0.596	0.292		+	+		+	0.251			11	-320.2	663.7	3.3	0.03	0.25	0.28
	-0.578	0.320	0.152	+		+	+	0.259			12	-319.2	663.9	3.4	0.03	0.27	0.29
	-0.588	0.319	0.146	+			+	0.255		-0.016	12	-319.2	663.9	3.5	0.03	0.27	0.29
	-0.604	0.283	0.156	+	+	+	+	0.243	+		15	-315.9	664.2	3.8	0.02	0.28	0.30
	-0.615	0.285	0.149	+	+		+	0.238	+	-0.020	15	-315.9	664.3	3.8	0.02	0.28	0.30
	-0.529	0.290		+		+	+	0.264			11	-320.5	664.3	3.8	0.02	0.25	0.27

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.551	0.248		+	+	+	+	0.248	+		14	-317.3	664.8	4.3	0.02	0.25	0.28
	-0.549	0.273	0.147	+		+	+	0.253	+	-0.016	15	-316.2	664.9	4.4	0.02	0.28	0.29
	-0.325	0.137		+				0.259	+		11	-320.9	665.0	4.5	0.02	0.22	0.28
	-0.627	0.322	0.154	+	+	+	+	0.248			13	-318.8	665.3	4.9	0.01	0.27	0.29
	-0.636	0.320	0.147	+	+		+	0.243		-0.020	13	-318.8	665.4	4.9	0.01	0.27	0.29
	-0.576	0.292		+	+	+	+	0.253			12	-320.1	665.8	5.3	0.01	0.25	0.28
	-0.571	0.319	0.145	+		+	+	0.257		-0.016	13	-319.1	666.1	5.6	0.01	0.27	0.29
	-0.350	0.189		+				0.264			9	-323.7	666.2	5.7	0.01	0.22	0.28
	-0.597	0.282	0.148	+	+	+	+	0.240	+	-0.019	16	-315.9	666.5	6.0	0.01	0.28	0.30
	-0.326	0.154	0.079	+				0.258	+		12	-320.5	666.6	6.1	0.01	0.24	0.29
	-0.370	0.146		+	+			0.247	+		12	-320.5	666.6	6.1	0.01	0.22	0.28
	-0.300	0.132		+		+		0.262	+		12	-320.7	667.0	6.5	0.01	0.22	0.28
	$\sum w_i$	**0.99**	0.61	**1**	0.32	0.26	0.36	**1**	0.64	0.15							
250																	
	-0.353	0.271	0.168	+				0.270			10	-321.7	664.4	0.0	0.12	0.26	0.29
	-0.437	0.272	0.183	+			+	0.276			11	-321.1	665.5	1.0	0.07	0.26	0.29
	-0.352	0.217		+				0.274			9	-323.4	665.6	1.2	0.07	0.23	0.27
	-0.400	0.273	0.170	+	+			0.259			11	-321.3	665.9	1.5	0.06	0.26	0.29
	-0.336	0.283	0.208	+				0.270		0.073	11	-321.5	666.3	1.9	0.05	0.26	0.28
	-0.332	0.270	0.167	+		+		0.272			11	-321.6	666.5	2.0	0.04	0.26	0.29
	-0.354	0.286	0.171	+				0.265	+		12	-320.6	666.8	2.4	0.04	0.27	0.29
	-0.482	0.274	0.185	+	+		+	0.265			12	-320.7	667.0	2.6	0.03	0.27	0.29
	-0.398	0.219		+	+			0.263			10	-323.0	667.1	2.7	0.03	0.23	0.28
	-0.417	0.217		+			+	0.279			10	-323.0	667.1	2.7	0.03	0.23	0.27
	-0.416	0.271	0.182	+		+	+	0.277			12	-321.0	667.5	3.1	0.03	0.26	0.29
	-0.329	0.217		+		+		0.276			10	-323.2	667.6	3.2	0.03	0.23	0.28
	-0.423	0.277	0.198	+			+	0.275		0.029	12	-321.1	667.7	3.2	0.02	0.26	0.29
	-0.384	0.285	0.210	+	+			0.259		0.073	12	-321.1	667.8	3.4	0.02	0.26	0.29
	-0.439	0.287	0.187	+			+	0.271	+		13	-320.0	667.9	3.5	0.02	0.27	0.29
	-0.380	0.272	0.169	+	+	+		0.261			12	-321.2	668.0	3.5	0.02	0.26	0.29
	-0.352	0.229		+				0.268	+		11	-322.4	668.0	3.6	0.02	0.23	0.28

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R^2m	R^2c
	-0.358			+				0.280			8	-325.8	668.2	3.8	0.02	0.17	0.28
	-0.402	0.293	0.173	+	+			0.254	+		13	-320.3	668.4	4.0	0.02	0.27	0.30
	-0.315	0.282	0.207	+		+		0.272		0.073	12	-321.4	668.4	4.0	0.02	0.26	0.29
	-0.461	0.219		+	+		+	0.268			11	-322.7	668.7	4.2	0.01	0.23	0.27
	-0.338	0.298	0.210	+				0.265	+	0.071	13	-320.5	668.8	4.4	0.01	0.26	0.29
	-0.333	0.283	0.170	+		+		0.267	+		13	-320.6	668.9	4.5	0.01	0.27	0.29
	-0.375	0.219		+	+	+		0.266			11	-322.9	669.1	4.7	0.01	0.23	0.28
	-0.462	0.274	0.184	+	+	+	+	0.267			13	-320.6	669.1	4.7	0.01	0.27	0.29
	-0.394	0.216		+		+	+	0.281			11	-322.9	669.1	4.7	0.01	0.23	0.27
	-0.468	0.279	0.200	+	+		+	0.265		0.029	13	-320.7	669.2	4.8	0.01	0.27	0.29
	-0.485	0.293	0.188	+	+		+	0.260	+		14	-319.7	669.5	5.1	0.01	0.27	0.30
	-0.359		0.107	+				0.279			9	-325.3	669.6	5.1	0.01	0.19	0.29
	-0.398	0.235		+	+			0.257	+		12	-322.0	669.6	5.2	0.01	0.24	0.28
	-0.417	0.227		+			+	0.274	+		12	-322.0	669.6	5.2	0.01	0.24	0.28
	-0.402			+	+			0.270			9	-325.4	669.7	5.3	0.01	0.17	0.29
	-0.402	0.276	0.197	+		+	+	0.277		0.030	13	-321.0	669.7	5.3	0.01	0.26	0.29
	-0.426			+			+	0.285			9	-325.5	669.8	5.4	0.01	0.18	0.28
	-0.363	0.285	0.209	+	+	+		0.261		0.073	13	-321.0	669.9	5.5	0.01	0.26	0.29
	-0.418	0.283	0.186	+		+	+	0.273	+		14	-320.0	670.0	5.6	0.01	0.27	0.29
	-0.329	0.225		+		+		0.271	+		12	-322.3	670.1	5.7	0.01	0.23	0.28
	-0.333			+		+		0.283			9	-325.6	670.1	5.7	0.01	0.18	0.29
	-0.426	0.291	0.200	+			+	0.271	+	0.027	14	-320.0	670.1	5.7	0.01	0.27	0.29
	-0.385	0.305	0.212	+	+			0.254	+	0.071	14	-320.1	670.3	5.9	0.01	0.27	0.30
	-0.381	0.290	0.172	+	+	+		0.256	+		14	-320.2	670.5	6.1	0.01	0.27	0.30
	-0.439	0.218		+	+	+	+	0.271			12	-322.6	670.7	6.3	0.01	0.23	0.28
	-0.445		0.128	+			+	0.285			10	-324.9	670.9	6.5	0.00	0.19	0.29
	-0.317	0.294	0.209	+		+		0.267	+	0.072	14	-320.4	670.9	6.5	0.00	0.27	0.29
	-0.403		0.107	+	+			0.269			10	-325.0	671.1	6.7	0.00	0.19	0.29
	-0.462	0.234		+	+		+	0.263	+		13	-321.7	671.2	6.8	0.00	0.24	0.28
	-0.448	0.279	0.199	+	+	+	+	0.267		0.030	14	-320.6	671.3	6.9	0.00	0.27	0.29
	-0.469			+	+		+	0.275			10	-325.2	671.4	7.0	0.00	0.18	0.29
	$\sum w_i$	**0.86**	0.53	1	0.25	0.3	0.37	**1**	0.19	0.11							

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R^{2}m	R^{2}c
500																	
	-0.358			+				0.280			8	-325.8	668.2	0.0	0.11	0.17	0.28
	-0.360	0.132		+				0.285			9	-325.0	668.9	0.7	0.08	0.19	0.28
	-0.402			+	+			0.270			9	-325.4	669.7	1.5	0.05	0.17	0.29
	-0.360	0.170	0.132	+				0.284			10	-324.3	669.8	1.6	0.05	0.21	0.28
	-0.426			+			+	0.285			9	-325.5	669.8	1.6	0.05	0.18	0.28
	-0.461	0.162		+			+	0.293			10	-324.4	669.9	1.7	0.05	0.20	0.28
	-0.358		0.083	+				0.277			9	-325.5	669.9	1.7	0.05	0.18	0.29
	-0.333			+		+		0.283			9	-325.6	670.1	1.9	0.04	0.18	0.29
	-0.478	0.202	0.147	+			+	0.292			11	-323.6	670.4	2.2	0.04	0.22	0.28
	-0.403	0.133		+	+			0.275			10	-324.7	670.5	2.3	0.04	0.19	0.28
	-0.335	0.132		+		+		0.288			10	-324.9	670.9	2.7	0.03	0.19	0.27
	-0.403	0.171	0.133	+	+			0.273			11	-324.0	671.3	3.1	0.02	0.21	0.28
	-0.469			+	+		+	0.275			10	-325.2	671.4	3.2	0.02	0.18	0.29
	-0.402		0.084	+	+			0.267			10	-325.2	671.5	3.3	0.02	0.18	0.29
	-0.432		0.089	+			+	0.282			10	-325.2	671.5	3.3	0.02	0.19	0.29
	-0.503	0.163		+	+		+	0.283			11	-324.1	671.5	3.3	0.02	0.20	0.28
	-0.377			+	+	+		0.272			10	-325.3	671.7	3.5	0.02	0.18	0.29
	-0.336	0.170	0.131	+		+		0.286			11	-324.2	671.7	3.5	0.02	0.21	0.28
	-0.402			+		+	+	0.287			10	-325.3	671.8	3.6	0.02	0.18	0.28
	-0.381	0.174	0.118	+				0.282		-0.078	11	-324.2	671.8	3.6	0.02	0.22	0.28
	-0.333		0.083	+		+		0.280			10	-325.4	671.9	3.7	0.02	0.19	0.29
	-0.436	0.162		+		+	+	0.296			11	-324.3	671.9	3.7	0.02	0.20	0.28
	-0.520	0.203	0.148	+	+		+	0.282			12	-323.3	672.0	3.8	0.02	0.22	0.28
	-0.454	0.202	0.146	+		+	+	0.294			12	-323.4	672.4	4.2	0.01	0.22	0.28
	-0.379	0.132		+	+	+		0.278			11	-324.6	672.5	4.3	0.01	0.19	0.28
	-0.490	0.203	0.137	+			+	0.291		-0.053	12	-323.5	672.6	4.4	0.01	0.22	0.28
	-0.371	0.202		+				0.285	+		11	-324.7	672.6	4.4	0.01	0.20	0.28
	-0.474		0.090	+	+		+	0.272			11	-324.9	673.1	4.9	0.01	0.19	0.29
	-0.426	0.174	0.119	+	+			0.272		-0.080	12	-323.9	673.4	5.2	0.01	0.22	0.29
	-0.379	0.170	0.132	+	+	+		0.276			12	-323.9	673.4	5.2	0.01	0.21	0.29

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.444			+	+	+	+	0.277			11	-325.0	673.4	5.2	0.01	0.18	0.29
	-0.407		0.089	+		+	+	0.285			11	-325.1	673.4	5.2	0.01	0.19	0.29
	-0.377		0.084	+	+	+		0.270			11	-325.1	673.4	5.2	0.01	0.19	0.29
	-0.371	0.240	0.132	+				0.283	+		12	-324.0	673.5	5.3	0.01	0.22	0.29
	-0.479	0.163		+	+	+	+	0.286			12	-324.0	673.5	5.3	0.01	0.19	0.27
	-0.473	0.231		+			+	0.293	+		12	-324.0	673.6	5.4	0.01	0.21	0.28
	-0.357	0.174	0.117	+		+		0.285		-0.077	12	-324.1	673.8	5.6	0.01	0.22	0.29
	-0.496	0.202	0.147	+	+	+	+	0.284			13	-323.1	674.1	5.9	0.01	0.22	0.28
	-0.490	0.270	0.147	+			+	0.292	+		13	-323.2	674.2	6.0	0.01	0.23	0.29
	-0.415	0.205		+	+			0.274	+		12	-324.3	674.2	6.0	0.01	0.19	0.28
	-0.533	0.204	0.138	+	+		+	0.281		-0.055	13	-323.2	674.2	6.0	0.01	0.22	0.29
	-0.466	0.203	0.137	+		+	+	0.293		-0.052	13	-323.4	674.6	6.4	0.00	0.22	0.28
	-0.347	0.201		+		+		0.287	+		12	-324.5	674.6	6.4	0.00	0.20	0.28
	-0.450		0.090	+	+	+	+	0.274			12	-324.8	675.1	6.9	0.00	0.18	0.29
	-0.416	0.243	0.134	+	+			0.272	+		13	-323.6	675.1	6.9	0.00	0.22	0.29
	$\sum w_i$	0.55	0.40	**1**	0.31	0.27	0.36	**1**	0.07	0.07							
1000																	
	-0.358			+				0.280			8	-325.8	668.2	0.0	0.19	0.17	0.28
	-0.402			+	+			0.270			9	-325.4	669.7	1.5	0.09	0.17	0.29
	-0.426			+			+	0.285			9	-325.5	669.8	1.6	0.08	0.18	0.28
	-0.333			+		+		0.283			9	-325.6	670.1	1.9	0.07	0.18	0.29
	-0.357	-0.035		+				0.278			9	-325.7	670.3	2.1	0.07	0.18	0.29
	-0.357		0.026	+				0.278			9	-325.7	670.3	2.1	0.06	0.18	0.29
	-0.469			+	+		+	0.275			10	-325.2	671.4	3.2	0.04	0.18	0.29
	-0.377			+	+	+		0.272			10	-325.3	671.7	3.5	0.03	0.18	0.29
	-0.402			+		+	+	0.287			10	-325.3	671.8	3.6	0.03	0.18	0.28
	-0.401	-0.037		+	+			0.268			10	-325.4	671.8	3.6	0.03	0.18	0.29
	-0.401		0.028	+	+			0.268			10	-325.4	671.9	3.7	0.03	0.18	0.29
	-0.432		0.041	+			+	0.282			10	-325.4	671.9	3.7	0.03	0.18	0.29
	-0.424	-0.010		+			+	0.284			10	-325.5	672.0	3.8	0.03	0.18	0.28
	-0.333	-0.034		+		+		0.281			10	-325.6	672.3	4.1	0.02	0.18	0.29

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.333		0.025	+		+		0.281			10	-325.6	672.3	4.1	0.02	0.18	0.29
	-0.357	-0.030	0.009	+				0.278			10	-325.7	672.5	4.3	0.02	0.18	0.29
	-0.260	0.064	0.133	+				0.283		0.218	11	-325.0	673.3	5.1	0.01	0.19	0.29
	-0.444			+	+	+	+	0.277			11	-325.0	673.4	5.2	0.01	0.18	0.29
	-0.475		0.044	+	+		+	0.272			11	-325.1	673.5	5.3	0.01	0.18	0.29
	-0.466	-0.012		+	+		+	0.274			11	-325.1	673.6	5.4	0.01	0.18	0.29
	-0.377	-0.036		+	+	+		0.270			11	-325.3	673.8	5.6	0.01	0.18	0.29
	-0.377		0.028	+	+	+		0.271			11	-325.3	673.9	5.7	0.01	0.18	0.29
	-0.407		0.041	+		+	+	0.285			11	-325.3	673.9	5.7	0.01	0.18	0.29
	-0.400	-0.009		+		+	+	0.287			11	-325.3	674.0	5.8	0.01	0.18	0.28
	-0.401	-0.031	0.011	+	+			0.267			11	-325.4	674.1	5.9	0.01	0.18	0.29
	-0.438	0.019	0.052	+			+	0.283			11	-325.4	674.1	5.9	0.01	0.18	0.28
	-0.354	0.154	0.223	+			+	0.293		0.278	12	-324.4	674.2	6.0	0.01	0.20	0.29
	-0.355	0.039		+				0.280	+		11	-325.5	674.3	6.1	0.01	0.18	0.29
	-0.333	-0.030	0.008	+		+		0.280			11	-325.6	674.5	6.3	0.01	0.18	0.29
	-0.304	0.065	0.137	+	+			0.272		0.219	12	-324.7	674.9	6.7	0.01	0.19	0.29
	$\sum w_i$	0.31	0.29	**1**	0.31	0.27	0.31	**1**	0.04	0.05							
2000																	
	-0.358			+				0.280			8	-325.8	668.2	0.0	0.17	0.17	0.28
	-0.402			+	+			0.270			9	-325.4	669.7	1.5	0.08	0.17	0.29
	-0.426			+			+	0.285			9	-325.5	669.8	1.6	0.08	0.18	0.28
	-0.357		0.074	+				0.276			9	-325.6	670.0	1.8	0.07	0.18	0.28
	-0.357	-0.061		+				0.277			9	-325.6	670.1	1.9	0.07	0.18	0.29
	-0.333			+		+		0.283			9	-325.6	670.1	1.9	0.07	0.18	0.29
	-0.469			+	+		+	0.275			10	-325.2	671.4	3.2	0.04	0.18	0.29
	-0.401		0.076	+	+			0.266			10	-325.2	671.5	3.3	0.03	0.18	0.29
	-0.431		0.081	+			+	0.281			10	-325.2	671.6	3.4	0.03	0.19	0.29
	-0.401	-0.063		+	+			0.267			10	-325.3	671.7	3.5	0.03	0.18	0.29
	-0.377			+	+	+		0.272			10	-325.3	671.7	3.5	0.03	0.18	0.29
	-0.402			+		+	+	0.287			10	-325.3	671.8	3.6	0.03	0.18	0.28
	-0.419	-0.047		+			+	0.282			10	-325.4	671.9	3.7	0.03	0.18	0.29

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R^2m	R^2c
	-0.332		0.074	+		+		0.279			10	-325.4	672.0	3.8	0.03	0.18	0.29
	-0.332	-0.061		+		+		0.280			10	-325.5	672.1	3.9	0.02	0.18	0.29
	-0.356	-0.043	0.061	+				0.275			10	-325.5	672.1	3.9	0.02	0.19	0.29
	-0.310	-0.068	0.086	+				0.278		0.155	11	-324.6	672.4	4.2	0.02	0.21	0.30
	-0.474		0.083	+	+		+	0.270			11	-324.9	673.1	4.9	0.01	0.19	0.29
	-0.444			+	+	+	+	0.277			11	-325.0	673.4	5.2	0.01	0.18	0.29
	-0.462	-0.049		+	+		+	0.272			11	-325.1	673.4	5.2	0.01	0.18	0.29
	-0.407		0.081	+		+	+	0.283			11	-325.1	673.5	5.3	0.01	0.19	0.29
	-0.376		0.076	+	+	+		0.268			11	-325.1	673.5	5.3	0.01	0.18	0.29
	-0.400	-0.044	0.062	+	+			0.264			11	-325.2	673.6	5.4	0.01	0.19	0.29
	-0.376	-0.063		+	+	+		0.269			11	-325.2	673.6	5.4	0.01	0.18	0.29
	-0.427	-0.024	0.074	+			+	0.280			11	-325.2	673.7	5.5	0.01	0.19	0.29
	-0.394	-0.047		+		+	+	0.285			11	-325.3	673.8	5.6	0.01	0.18	0.29
	-0.354	-0.069	0.087	+	+			0.267		0.155	12	-324.2	674.0	5.8	0.01	0.21	0.31
	-0.378	-0.047	0.101	+			+	0.283		0.157	12	-324.2	674.0	5.8	0.01	0.21	0.31
	-0.331	-0.043	0.061	+		+		0.277			11	-325.4	674.1	5.9	0.01	0.19	0.29
	-0.287	-0.068	0.085	+		+		0.280		0.154	12	-324.4	674.4	6.2	0.01	0.21	0.31
	-0.355	-0.042		+				0.278	+		11	-325.6	674.5	6.3	0.01	0.18	0.29
	-0.450		0.083	+	+	+	+	0.273			12	-324.8	675.1	6.9	0.01	0.18	0.28
	$\sum w_i$	0.33	0.33	**1**	0.31	0.27	0.31	**1**	0.03	0.06							
3000																	
	-0.358			+				0.280			8	-325.8	668.2	0.0	0.16	0.17	0.28
	-0.356		0.114	+				0.274			9	-325.3	669.5	1.3	0.09	0.19	0.29
	-0.402			+	+			0.270			9	-325.4	669.7	1.5	0.08	0.17	0.29
	-0.426			+			+	0.285			9	-325.5	669.8	1.6	0.07	0.18	0.28
	-0.333			+		+		0.283			9	-325.6	670.1	1.9	0.06	0.18	0.29
	-0.358	-0.011		+				0.280			9	-325.7	670.4	2.2	0.06	0.18	0.28
	-0.400		0.116	+	+			0.263			10	-325.0	671.0	2.8	0.04	0.19	0.29
	-0.428		0.117	+			+	0.278			10	-325.0	671.0	2.8	0.04	0.19	0.29
	-0.469			+	+		+	0.275			10	-325.2	671.4	3.2	0.03	0.18	0.29
	-0.331		0.114	+		+		0.276			10	-325.2	671.4	3.2	0.03	0.19	0.29

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.356	0.016	0.118	+				0.274			10	-325.3	671.6	3.4	0.03	0.19	0.29
	-0.377			+	+	+		0.272			10	-325.3	671.7	3.5	0.03	0.18	0.29
	-0.402			+		+	+	0.287			10	-325.3	671.8	3.6	0.03	0.18	0.28
	-0.402	-0.012		+	+			0.269			10	-325.4	671.9	3.7	0.03	0.18	0.29
	-0.427	0.004		+			+	0.285			10	-325.5	672.0	3.8	0.02	0.18	0.28
	-0.333	-0.011		+		+		0.282			10	-325.6	672.3	4.1	0.02	0.18	0.29
	-0.471		0.119	+	+		+	0.268			11	-324.7	672.6	4.4	0.02	0.20	0.29
	-0.376		0.116	+	+	+		0.266			11	-324.8	673.0	4.8	0.01	0.19	0.29
	-0.403		0.117	+		+	+	0.281			11	-324.9	673.0	4.8	0.01	0.20	0.29
	-0.433	0.032	0.125	+			+	0.280			11	-325.0	673.2	5.0	0.01	0.19	0.29
	-0.400	0.015	0.120	+	+			0.264			11	-325.0	673.2	5.0	0.01	0.19	0.29
	-0.444			+	+	+	+	0.277			11	-325.0	673.4	5.2	0.01	0.18	0.29
	-0.332	0.032	0.131	+				0.276		0.099	11	-325.0	673.4	5.2	0.01	0.20	0.29
	-0.469	0.003		+	+		+	0.275			11	-325.2	673.6	5.4	0.01	0.18	0.29
	-0.331	0.016	0.118	+		+		0.277			11	-325.2	673.6	5.4	0.01	0.19	0.29
	-0.377	-0.012		+	+	+		0.272			11	-325.3	673.9	5.7	0.01	0.18	0.29
	-0.402	0.004		+		+	+	0.287			11	-325.3	674.0	5.8	0.01	0.18	0.28
	-0.364	-0.066		+				0.279	+		11	-325.6	674.4	6.2	0.01	0.18	0.29
	-0.447		0.119	+	+	+	+	0.270			12	-324.5	674.6	6.4	0.01	0.20	0.30
	-0.413	0.056	0.143	+			+	0.283		0.119	12	-324.6	674.8	6.6	0.01	0.20	0.30
	-0.476	0.031	0.127	+	+		+	0.269			12	-324.6	674.8	6.6	0.01	0.20	0.29
	-0.377	0.032	0.133	+	+			0.266		0.100	12	-324.7	675.0	6.8	0.01	0.20	0.30
	-0.408	0.033	0.125	+		+	+	0.282			12	-324.8	675.2	7.0	0.00	0.20	0.29
	$\sum w_i$	0.3	0.37	**1**	0.31	0.27	0.31	**1**	0.03	0.04							
Parasitism rate																	
100																	
	-0.357			NA				0.621	NA	-	5	-108.3	227.4	0.0	0.1	0.14	0.32
	-0.099			NA		+		0.663	NA	-	6	-107.3	228.0	0.6	0.1	0.16	0.34
	-0.585			NA			+	0.656	NA	-	6	-107.6	228.6	1.2	0.1	0.16	0.31
	-0.479			-	+			0.610	-	NA	6	-107.8	228.8	1.4	0.1	0.16	0.35
	-0.342			-		+	+	0.702	-	NA	7	-106.7	229.2	1.8	0.1	0.19	0.33

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.222			-	+	+		0.651	-	NA	7	-106.9	229.5	2.1	0.1	0.18	0.36
	-0.357	0.041		-				0.620	-	NA	6	-108.2	229.8	2.3	0.0	0.14	0.32
	-0.357		-0.002	-				0.621	-	NA	6	-108.3	229.8	2.4	0.0	0.14	0.32
	-0.710			-	+		+	0.647	-	NA	7	-107.1	230.0	2.6	0.0	0.19	0.34
	-0.708	0.229		-			+	0.667	-	NA	7	-107.2	230.1	2.7	0.0	0.17	0.33
	-0.476	0.291		-		+	+	0.723	-	NA	8	-106	230.3	2.9	0.0	0.20	0.36
	-0.090	0.081		-		+		0.662	-	NA	7	-107.3	230.3	2.9	0.0	0.16	0.34
	-0.099		-0.031	-		+		0.666	-	NA	7	-107.3	230.4	3.0	0.0	0.16	0.34
	-0.468			-	+	+	+	0.691	-	NA	8	-106.3	230.8	3.4	0.0	0.21	0.36
	-0.587		0.033	-			+	0.655	-	NA	7	-107.6	231.0	3.6	0.0	0.17	0.30
	-0.480	0.048		-	+			0.609	-	NA	7	-107.7	231.2	3.8	0.0	0.16	0.35
	-0.479		-0.006	-	+			0.611	-	NA	7	-107.8	231.3	3.9	0.0	0.16	0.34
	-0.849	0.244		-	+		+	0.657	-	NA	8	-106.6	231.5	4.1	0.0	0.20	0.36
	-0.343		0.008	-		+	+	0.701	-	NA	8	-106.7	231.8	4.3	0.0	0.19	0.33
	-0.620	0.306		-	+	+	+	0.713	-	NA	9	-105.5	231.8	4.4	0.0	0.22	0.39
	-0.213	0.089		-	+	+		0.650	-	NA	8	-106.8	231.9	4.5	0.0	0.18	0.37
	-0.222		-0.035	-	+	+		0.654	-	NA	8	-106.9	232.0	4.6	0.0	0.18	0.36
	-0.357	0.041	0.000	-				0.620	-	NA	7	-108.2	232.2	4.8	0.0	0.14	0.31
	-0.712		0.028	-	+		+	0.645	-	NA	8	-107.1	232.6	5.1	0.0	0.19	0.33
	-0.717	0.236	0.067	-			+	0.664	-	NA	8	-107.1	232.6	5.2	0.0	0.17	0.32
	-0.090	0.081	-0.029	-		+		0.665	-	NA	8	-107.3	232.8	5.4	0.0	0.16	0.34
	-0.484	0.296	0.047	-		+	+	0.721	-	NA	9	-106	232.9	5.5	0.0	0.20	0.35
	-0.469		0.004	-	+	+	+	0.690	-	NA	9	-106.3	233.4	6.0	0.0	0.21	0.35
	-0.480	0.048	-0.004	-	+			0.609	-	NA	8	-107.7	233.7	6.3	0.0	0.16	0.34
	-0.857	0.251	0.063	-	+		+	0.655	-	NA	9	-106.6	234.1	6.7	0.0	0.20	0.35
	$\sum w_i$	0.29	0.24	-	0.22	0.25	0.36	**1**	-	NA							
250m																	
	-0.357			-				0.621	-		5	-108.3	227.4	0.0	0.2	0.14	0.32
	-0.099			-		+		0.663	-		6	-107.3	228.0	0.6	0.1	0.16	0.34
	-0.585			-			+	0.656	-		6	-107.6	228.6	1.2	0.1	0.16	0.31
	-0.479			-	+			0.610	-		6	-107.8	228.8	1.4	0.1	0.16	0.35

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.342			-		+	+	0.702	-		7	-106.7	229.2	1.8	0.1	0.19	0.33
	-0.222			-	+	+		0.651	-		7	-106.9	229.5	2.1	0.1	0.18	0.36
	-0.357	0.055		-				0.622	-		6	-108.2	229.7	2.3	0.1	0.14	0.32
	-0.359		-0.038	-				0.624	-		6	-108.2	229.8	2.4	0.0	0.14	0.32
	-0.710			-	+		+	0.647	-		7	-107.1	230.0	2.6	0.0	0.19	0.34
	-0.095	0.074		-		+		0.664	-		7	-107.3	230.3	2.9	0.0	0.16	0.34
	-0.099		-0.063	-		+		0.668	-		7	-107.3	230.4	3.0	0.0	0.16	0.34
	-0.468			-	+	+	+	0.691	-		8	-106.3	230.8	3.4	0.0	0.21	0.36
	-0.586	0.054		-			+	0.656	-		7	-107.6	231.0	3.6	0.0	0.16	0.31
	-0.584		-0.010	-			+	0.657	-		7	-107.6	231.0	3.6	0.0	0.16	0.31
	-0.482	0.068		-	+			0.611	-		7	-107.7	231.2	3.8	0.0	0.16	0.35
	-0.482		-0.045	-	+			0.613	-		7	-107.7	231.2	3.8	0.0	0.16	0.35
	-0.338	0.073		-		+	+	0.702	-		8	-106.7	231.6	4.2	0.0	0.19	0.33
	-0.339		-0.033	-		+	+	0.703	-		8	-106.7	231.7	4.3	0.0	0.19	0.33
	-0.219	0.088		-	+	+		0.652	-		8	-106.8	231.9	4.5	0.0	0.18	0.37
	-0.223		-0.070	-	+	+		0.656	-		8	-106.8	232.0	4.6	0.0	0.18	0.37
	-0.359	0.048	-0.022	-				0.623	-		7	-108.2	232.2	4.8	0.0	0.14	0.32
	-0.714	0.068		-	+		+	0.646	-		8	-107.1	232.5	5.1	0.0	0.19	0.34
	-0.710		-0.018	-	+		+	0.647	-		8	-107.1	232.6	5.1	0.0	0.19	0.34
	-0.096	0.062	-0.043	-		+		0.667	-		8	-107.3	232.8	5.4	0.0	0.16	0.34
	-0.467	0.087		-	+	+	+	0.690	-		9	-106.2	233.3	5.9	0.0	0.21	0.36
	-0.452	-0.041	-0.234	-				0.589	-	-0.404	8	-107.5	233.3	5.9	0.0	0.16	0.33
	-0.846	-0.054	-0.281	-			+	0.616	-	-0.589	9	-106.2	233.4	6.0	0.0	0.21	0.31
	-0.465		-0.041	-	+	+	+	0.693	-		9	-106.2	233.4	6.0	0.0	0.21	0.36
	-0.586	0.056	0.008	-			+	0.656	-		8	-107.6	233.5	6.1	0.0	0.16	0.31
	-0.483	0.061	-0.025	-	+			0.613	-		8	-107.7	233.7	6.3	0.0	0.16	0.35
	-0.184	-0.030	-0.275	-		+		0.629	-	-0.449	9	-106.5	233.8	6.4	0.0	0.19	0.35
	-0.595	-0.042	-0.320	-		+	+	0.657	-	-0.633	10	-105.2	234.0	6.6	0.0	0.24	0.33
	-0.338	0.070	-0.009	-		+	+	0.702	-		9	-106.7	234.3	6.9	0.0	0.19	0.33
	$\sum w_i$	0.26	0.26	-	0.32	0.32	0.35	**1**	-	0.04							

500m

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.804	-0.213	-0.733	-				0.589	-	-1.311	8	-103.5	225.2	0.0	0.2	0.37	0.42
	-0.575	-0.203	-0.793	-		+		0.643	-	-1.37	9	-102.3	225.6	0.3	0.1	0.40	0.45
	-1.051	-0.153	-0.732	-			+	0.631	-	-1.337	9	-102.8	226.5	1.3	0.1	0.40	0.43
	-0.831	-0.143	-0.793	-		+	+	0.687	-	-1.396	10	-101.7	226.9	1.7	0.1	0.42	0.46
	-0.909	-0.209	-0.733	-	+			0.583	-	-1.295	9	-103.1	227.0	1.8	0.1	0.37	0.44
	-0.357			-				0.621	-		5	-108.3	227.4	2.2	0.1	0.14	0.32
	-0.677	-0.198	-0.792	-	+	+		0.635	-	-1.352	10	-102	227.5	2.3	0.1	0.40	0.47
	-0.099			-		+		0.663	-		6	-107.3	228.0	2.8	0.0	0.16	0.34
	-1.163	-0.148	-0.733	-	+		+	0.626	-	-1.322	10	-102.4	228.4	3.2	0.0	0.40	0.45
	-0.585			-			+	0.656	-		6	-107.6	228.6	3.4	0.0	0.16	0.31
	-0.479			-	+			0.610	-		6	-107.8	228.8	3.6	0.0	0.16	0.35
	-0.371		-0.238	-				0.652	-		6	-107.8	228.9	3.7	0.0	0.15	0.34
	-0.941	-0.137	-0.793	-	+	+	+	0.681	-	-1.38	11	-101.3	229.0	3.8	0.0	0.43	0.47
	-0.097		-0.289	-		+		0.705	-		7	-106.7	229.2	4.0	0.0	0.18	0.37
	-0.342			-		+	+	0.702	-		7	-106.7	229.2	4.0	0.0	0.19	0.33
	-0.222			-	+	+		0.651	-		7	-106.9	229.5	4.3	0.0	0.18	0.36
	-0.357	-0.006		-				0.621	-		6	-108.2	229.8	4.6	0.0	0.14	0.32
	-0.710			-	+		+	0.647	-		7	-107.1	230.0	4.8	0.0	0.19	0.34
	-0.606		-0.257	-			+	0.689	-		7	-107.1	230.0	4.8	0.0	0.17	0.33
	-0.497		-0.246	-	+			0.642	-		7	-107.3	230.3	5.1	0.0	0.17	0.37
	-0.350		-0.310	-		+	+	0.745	-		8	-106.1	230.4	5.2	0.0	0.20	0.36
	-0.099	0.013		-		+		0.664	-		7	-107.3	230.4	5.2	0.0	0.16	0.34
	-0.222		-0.295	-	+	+		0.693	-		8	-106.2	230.8	5.5	0.0	0.19	0.39
	-0.468			-	+	+	+	0.691	-		8	-106.3	230.8	5.6	0.0	0.21	0.36
	-0.594	0.042		-			+	0.659	-		7	-107.6	231.0	5.8	0.0	0.16	0.31
	-0.370	-0.121	-0.293	-				0.651	-		7	-107.7	231.1	5.9	0.0	0.15	0.34
	-0.479	0.000		-	+			0.610	-		7	-107.8	231.3	6.0	0.0	0.16	0.35
	-0.737		-0.267	-	+		+	0.680	-		8	-106.6	231.5	6.3	0.0	0.20	0.36
	-0.103	-0.120	-0.345	-		+		0.705	-		8	-106.6	231.6	6.3	0.0	0.18	0.37
	-0.351	0.065		-		+	+	0.706	-		8	-106.7	231.7	6.5	0.0	0.18	0.33
	-0.482		-0.319	-	+	+	+	0.735	-		9	-105.6	232.0	6.8	0.0	0.22	0.39
	-0.221	0.020		-	+	+		0.652	-		8	-106.9	232.0	6.8	0.0	0.18	0.36

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	$\sum w_i$	**(0.69)**	**(0.73)**	-	0.3	0.34	0.34	**1**	-	**0.6**							
1000m																	
	-0.357			-				0.621	-		5	-108.3	227.4	0.0	0.1	0.14	0.32
	-0.099			-		+		0.663	-		6	-107.3	228.0	0.6	0.1	0.16	0.34
	-0.370	0.291		-				0.657	-		6	-107.4	228.2	0.8	0.1	0.16	0.34
	-0.369		-0.330	-				0.697	-		6	-107.5	228.2	0.8	0.1	0.15	0.35
	-0.091		-0.399	-		+		0.762	-		7	-106.3	228.4	1.0	0.1	0.18	0.37
	-0.717	0.398		-			+	0.723	-		7	-106.3	228.4	1.0	0.1	0.20	0.33
	-0.082	0.336		-		+		0.709	-		7	-106.4	228.5	1.1	0.1	0.19	0.36
	-0.585			-			+	0.656	-		6	-107.6	228.6	1.2	0.1	0.16	0.31
	-0.444	0.447		-		+	+	0.781	-		8	-105.2	228.7	1.3	0.0	0.23	0.35
	-0.479			-	+			0.610	-		6	-107.8	228.8	1.4	0.0	0.16	0.35
	-0.342			-		+	+	0.702	-		7	-106.7	229.2	1.8	0.0	0.19	0.33
	-0.222			-	+	+		0.651	-		7	-106.9	229.5	2.1	0.0	0.18	0.36
	-0.587		-0.330	-			+	0.731	-		7	-106.9	229.5	2.1	0.0	0.17	0.34
	-0.494		-0.333	-	+			0.686	-		7	-107	229.7	2.2	0.0	0.17	0.37
	-0.489	0.287		-	+			0.645	-		7	-107	229.7	2.3	0.0	0.17	0.36
	-0.323		-0.399	-		+	+	0.799	-		8	-105.8	229.8	2.4	0.0	0.20	0.37
	-0.216		-0.400	-	+	+		0.749	-		8	-105.8	230.0	2.6	0.0	0.19	0.40
	-0.839	0.395		-	+		+	0.711	-		8	-105.8	230.0	2.6	0.0	0.22	0.36
	-0.710			-	+		+	0.647	-		7	-107.1	230.0	2.6	0.0	0.19	0.34
	-0.202	0.331		-	+	+		0.695	-		8	-105.9	230.1	2.7	0.0	0.20	0.38
	-0.382	0.224	-0.162	-				0.694	-		7	-107.3	230.3	2.8	0.0	0.16	0.35
	-0.565	0.442		-	+	+	+	0.768	-		9	-104.8	230.4	3.0	0.0	0.24	0.38
	-0.084	0.246	-0.202	-		+		0.755	-		8	-106.1	230.5	3.1	0.0	0.19	0.37
	-0.468			-	+	+	+	0.691	-		8	-106.3	230.8	3.4	0.0	0.21	0.36
	-0.708	0.364	-0.070	-			+	0.736	-		8	-106.3	230.9	3.5	0.0	0.20	0.33
	-0.716		-0.336	-	+		+	0.721	-		8	-106.4	231.0	3.6	0.0	0.20	0.37
	-0.423	0.388	-0.111	-		+	+	0.801	-		9	-105.1	231.2	3.7	0.0	0.23	0.35
	-0.453		-0.403	-	+	+	+	0.787	-		9	-105.3	231.4	4.0	0.0	0.22	0.39
	-0.505	0.215	-0.171	-	+			0.683	-		8	-106.8	231.8	4.4	0.0	0.18	0.37

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.207	0.234	-0.214	-	+	+		0.742	-		9	-105.6	232.2	4.8	0.0	0.20	0.39
	-0.272	0.331	-0.040	-				0.712	-	0.233	8	-107.1	232.4	5.0	0.0	0.16	0.35
	-0.828	0.351	-0.085	-	+		+	0.726	-		9	-105.8	232.5	5.1	0.0	0.22	0.36
	-0.579	0.542	0.125	-			+	0.769	-	0.359	9	-105.8	232.6	5.2	0.0	0.21	0.34
	0.044	0.365	-0.071	-		+		0.777	-	0.261	9	-105.9	232.6	5.2	0.0	0.19	0.37
	-0.278	0.586	0.100	-		+	+	0.840	-	0.401	10	-104.6	232.8	5.4	0.0	0.24	0.36
	-0.545	0.375	-0.125	-	+	+	+	0.789	-		10	-104.7	232.9	5.5	0.0	0.24	0.38
	-0.389	0.331	-0.040	-	+			0.702	-	0.252	9	-106.5	234.0	6.6	0.0	0.18	0.38
	-0.699	0.543	0.123	-	+		+	0.760	-	0.382	10	-105.3	234.2	6.8	0.0	0.23	0.37
	-0.075	0.363	-0.071	-	+	+		0.765	-	0.278	10	-105.4	234.4	7.0	0.0	0.21	0.40
	$\sum w_i$	0.32	0.29	-	0.32	0.35	0.39	**1**	-	0.04							
2000m																	
	-0.503	0.689		-		+	+	0.873	-		8	-102.2	222.7	0.0	0.2	0.31	0.38
	-0.777	0.627		-			+	0.797	-		7	-103.7	223.2	0.4	0.1	0.27	0.36
	-0.065	0.556		-		+		0.767	-		7	-104.2	224.1	1.3	0.1	0.25	0.38
	-0.362	0.501		-				0.703	-		6	-105.5	224.3	1.6	0.1	0.21	0.35
	-0.610	0.681		-	+	+	+	0.860	-		9	-101.9	224.7	1.9	0.1	0.33	0.41
	-0.886	0.619		-	+		+	0.785	-		8	-103.3	224.9	2.2	0.1	0.29	0.38
	-0.510	0.704	0.063	-		+	+	0.859	-		9	-102.2	225.3	2.5	0.0	0.32	0.38
	-0.778	0.648	0.087	-			+	0.780	-		8	-103.6	225.5	2.8	0.0	0.28	0.35
	-0.431	0.685	0.057	-		+	+	0.912	-	0.259	10	-101	225.5	2.8	0.0	0.33	0.40
	-0.697	0.628	0.085	-			+	0.828	-	0.253	9	-102.5	225.8	3.1	0.0	0.30	0.37
	-0.173	0.547		-	+	+		0.753	-		8	-103.8	225.9	3.2	0.0	0.25	0.40
	-0.473	0.494		-	+			0.690	-		7	-105.1	226.0	3.2	0.0	0.22	0.38
	-0.065	0.561	0.022	-		+		0.762	-		8	-104.2	226.6	3.9	0.0	0.25	0.37
	-0.360	0.511	0.045	-				0.694	-		7	-105.5	226.7	4.0	0.0	0.21	0.35
	0.021	0.536	0.018	-		+		0.809	-	0.256	9	-103.2	227.2	4.5	0.0	0.26	0.39
	-0.614	0.693	0.053	-	+	+	+	0.849	-		10	-101.8	227.3	4.6	0.0	0.33	0.40
	-0.271	0.486	0.046	-				0.737	-	0.254	8	-104.5	227.3	4.6	0.0	0.22	0.36
	-0.885	0.638	0.076	-	+		+	0.771	-		9	-103.2	227.4	4.6	0.0	0.30	0.37
	-0.357			-				0.621	-		5	-108.3	227.4	4.7	0.0	0.14	0.32

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.546	0.672	0.044	-	+	+	+	0.904	-	0.271	11	-100.5	227.5	4.7	0.0	0.35	0.43
	-0.812	0.617	0.072	-	+		+	0.821	-	0.265	10	-102	227.6	4.9	0.0	0.32	0.40
	-0.099			-		+		0.663	-		6	-107.3	228.0	5.2	0.0	0.16	0.34
	-0.470	0.502	0.036	-	+			0.683	-		8	-105.1	228.5	5.7	0.0	0.22	0.37
	-0.173	0.550	0.013	-	+	+		0.750	-		9	-103.8	228.5	5.8	0.0	0.26	0.39
	-0.585			-			+	0.656	-		6	-107.6	228.6	5.8	0.0	0.16	0.31
	-0.479			-	+			0.610	-		6	-107.8	228.8	6.1	0.0	0.16	0.35
	-0.387	0.475	0.035	-	+			0.727	-	0.265	9	-104	229.0	6.3	0.0	0.24	0.39
	-0.093	0.523	0.008	-	+	+		0.797	-	0.267	10	-102.7	229.1	6.3	0.0	0.27	0.41
	-0.342			-		+	+	0.702	-		7	-106.7	229.2	6.5	0.0	0.19	0.33
	-0.222			-	+	+		0.651	-		7	-106.9	229.5	6.8	0.0	0.18	0.36
	-0.361		-0.097	-				0.640	-		6	-108.2	229.6	6.9	0.0	0.14	0.32
	$\sum w_i$	**0.92**	0.34	-	0.29	0.25	0.36	**1**	-	0.14							
3000m																	
	-0.361	0.427		-				0.657	-		6	-106.3	225.9	0.0	0.1	0.19	0.33
	-0.082	0.464		-		+		0.707	-		7	-105.1	226.0	0.2	0.1	0.23	0.35
	-0.686	0.491		-			+	0.714	-		7	-105.2	226.1	0.2	0.1	0.24	0.32
	-0.419	0.528		-		+	+	0.767	-		8	-104	226.3	0.5	0.1	0.26	0.34
	-0.357			-				0.621	-		5	-108.3	227.4	1.5	0.1	0.14	0.32
	-0.474	0.419		-	+			0.646	-		7	-105.9	227.5	1.6	0.0	0.21	0.35
	-0.799	0.484		-	+		+	0.703	-		8	-104.7	227.8	1.9	0.0	0.26	0.35
	-0.193	0.456		-	+	+		0.695	-		8	-104.8	227.8	2.0	0.0	0.24	0.37
	-0.099			-		+		0.663	-		6	-107.3	228.0	2.1	0.0	0.16	0.34
	-0.365	0.412	-0.074	-				0.672	-		7	-106.2	228.2	2.3	0.0	0.19	0.33
	-0.531	0.520		-	+	+	+	0.755	-		9	-103.7	228.2	2.3	0.0	0.28	0.36
	-0.079	0.446	-0.100	-		+		0.729	-		8	-105	228.4	2.5	0.0	0.23	0.36
	-0.688	0.479	-0.062	-			+	0.727	-		8	-105.1	228.5	2.6	0.0	0.24	0.32
	-0.585			-			+	0.656	-		6	-107.6	228.6	2.7	0.0	0.16	0.31
	-0.415	0.512	-0.089	-		+	+	0.787	-		9	-103.9	228.8	2.9	0.0	0.27	0.34
	-0.479			-	+			0.610	-		6	-107.8	228.8	2.9	0.0	0.16	0.35
	-0.342			-		+	+	0.702	-		7	-106.7	229.2	3.3	0.0	0.19	0.33

Scale	Intercept	CropDiv*	SNH*	S*	B*	F*†	SOC*†	A*	CropDiv:S*	CropDiv:SNH*	df	LogL	$AICc$	$\Delta AICc$	w_i	R²m	R²c
	-0.366		-0.167	-				0.652	-		6	-108	229.3	3.4	0.0	0.14	0.33
	-0.222			-	+	+		0.651	-		7	-106.9	229.5	3.6	0.0	0.18	0.36
	-0.096		-0.196	-		+		0.699	-		7	-107	229.8	3.9	0.0	0.17	0.35
	-0.479	0.403	-0.082	-	+			0.662	-		8	-105.8	229.9	4.0	0.0	0.21	0.36
	-0.710			-	+		+	0.647	-		7	-107.1	230.0	4.2	0.0	0.19	0.34
	-0.315	0.451	-0.075	-				0.685	-	0.198	8	-105.9	230.1	4.2	0.0	0.20	0.34
	-0.648	0.529	-0.063	-			+	0.747	-	0.226	9	-104.6	230.2	4.3	0.0	0.25	0.33
	-0.192	0.436	-0.108	-	+	+		0.718	-		9	-104.7	230.2	4.3	0.0	0.24	0.38
	-0.804	0.470	-0.072	-	+		+	0.718	-		9	-104.7	230.3	4.4	0.0	0.26	0.35
	-0.038	0.484	-0.102	-		+		0.742	-	0.188	9	-104.8	230.4	4.5	0.0	0.23	0.36
	-0.590		-0.162	-			+	0.682	-		7	-107.4	230.6	4.7	0.0	0.16	0.32
	-0.386	0.561	-0.091	-		+	+	0.807	-	0.22	10	-103.5	230.6	4.7	0.0	0.27	0.35
	-0.53	0.502	-0.098	-	+	+	+	0.777	-		10	-103.5	230.7	4.8	0.0	0.28	0.37
	-0.491		-0.174	-	+			0.641	-		7	-107.5	230.7	4.9	0.0	0.16	0.36
	-0.468			-	+	+	+	0.691	-		8	-106.3	230.8	4.9	0.0	0.21	0.36
	-0.335		-0.189	-		+	+	0.732	-		8	-106.5	231.2	5.3	0.0	0.19	0.34
	-0.221		-0.202	-	+	+		0.687	-		8	-106.5	231.4	5.5	0.0	0.18	0.38
	-0.430	0.443	-0.083	-	+			0.675	-	0.202	9	-105.5	231.8	6.0	0.0	0.22	0.36
	-0.766	0.521	-0.073	-	+		+	0.739	-	0.232	10	-104.2	232.0	6.1	0.0	0.27	0.36
	-0.719		-0.169	-	+		+	0.673	-		8	-106.9	232.1	6.2	0.0	0.19	0.35
	-0.152	0.474	-0.110	-	+	+		0.731	-	0.192	10	-104.4	232.3	6.4	0.0	0.25	0.38
	-0.502	0.552	-0.100	-	+	+	+	0.798	-	0.225	11	-103.1	232.6	6.7	0.0	0.29	0.38
	-0.464		-0.196	-	+	+	+	0.721	-		9	-106	232.8	7.0	0.0	0.21	0.37
	$\sum w_i$	**0.55**	0.26	-	0.22	0.25	0.35	**1.0**	-	0.04							

* A = Aphid density, B = Bird exclusion experiment (birds excluded yes/no), CropDiv = Crop diversity, F = Nitrogen fertilization (fertilizer applied yes/no), SNH = Proportion of seminatural habitat, SOC = soil organic carbon content (soil organic carbon content low/high), S = Survey interval (5 = day 0 to 5, 10 = days 5 to 10, 15 = days 10 to 15), CropDiv:S = interaction crop diversity x survey interval, CropDiv:SNH = Crop diversity x SNH interaction

† Nitrogen and SOC are included due to the nature of the experimental design and analysis, yet not further developed in this paper.

Table III.S6 Model-averaged estimates with unconditional lower and upper 95% confidence Intervals for biological control, predator density and parasitoid density as function of local and landscape factors on six spatial scales (100m, 250m, 500m, 1000m, 2000m, 3000m). Model averaging was based on a set of top models (ΔAICc<7). Estimates are highlighted in bold if 95% confidence intervals do not overlap zero.

Response	100	250	500	1000	2000	3000
Biological control						
CropDiv S5	-0.053 (-0.142, 0.036)	**-0.103 (-0.19, -0.015)**	**-0.1 (-0.187, -0.014)**	**-0.104 (-0.202, -0.016)**	-0.072 (-0.192, 0.01)	**-0.131 (-0.217, -0.045)**
CropDiv S10	0.085 (-0.1, 0.27)	0.048 (-0.136, 0.233)	0.057 (-0.124, 0.238)	0.017 (-0.17, 0.206)	-0.009 (-0.195, 0.203)	0.012 (-0.17, 0.194)
CropDiv S15	0.123 (-0.062, 0.307)	0.132 (-0.05, 0.314)	0.09 (-0.091, 0.272)	0.041 (-0.146, 0.234)	0.016 (-0.158, 0.244)	0.027 (-0.156, 0.211)
CropDiv:S5-S10	**0.139 (0.042, 0.235)**	**0.151 (0.054, 0.248)**	**0.157 (0.063, 0.251)**	**0.12 (0.032, 0.222)**	0.063 (-0.003, 0.194)	**0.143 (0.047, 0.239)**
CropDiv:S5-S15	**0.176 (0.081, 0.272)**	**0.235 (0.14, 0.33)**	**0.191 (0.096, 0.286)**	**0.145 (0.057, 0.25)**	**0.088 (0.035, 0.234)**	**0.158 (0.06, 0.256)**
CropDiv:S10-S15	0.038 (-0.059, 0.134)	0.084 (-0.015, 0.182)	0.033 (-0.064, 0.131)	0.025 (-0.222, 0.126)	0.025 (-0.064, 0.141)	0.015 (-0.087, 0.118)
SNH	-0.005 (-0.081, 0.046)	-0.003 (-0.079, 0.057)	-0.002 (-0.072, 0.061)	-0.027 (-0.12, 0.026)	-0.027 (-0.104, 0.016)	-0.021 (-0.094, 0.023)
CropDiv:SNH	-0.0001 (-0.068, 0.066)	0.0003 (-0.093, 0.103)	0.0141 (-0.034, 0.162)	-0.0011 (-0.111, 0.095)	-0.001 (-0.064, 0.048)	-0.0119 (-0.111, 0.027)
S5-S10	-0.029 (-0.127, 0.068)	-0.031 (-0.129, 0.068)	-0.03 (-0.127, 0.066)	-0.03 (-0.128, 0.069)	-0.027 (-0.128, 0.074)	-0.031 (-0.128, 0.067)
S5-S15	**0.254 (0.157, 0.351)**	**0.25 (0.154, 0.346)**	**0.254 (0.156, 0.351)**	**0.254 (0.153, 0.354)**	**0.259 (0.156, 0.362)**	**0.253 (0.154, 0.352)**
S10-S15	**0.284 (0.186, 0.382)**	**0.281 (0.181, 0.381)**	**0.284 (0.183, 0.384)**	**0.283 (0.18, 0.387)**	**0.286 (0.182, 0.39)**	**0.284 (0.18, 0.388)**
B	-0.029 (-0.141, 0.019)	-0.023 (-0.133, 0.026)	-0.029 (-0.141, 0.022)	-0.026 (-0.141, 0.026)	-0.023 (-0.139, 0.029)	-0.025 (-0.139, 0.027)
SOC	0.011 (-0.096, 0.17)	-0.005 (-0.138, 0.098)	-0.005 (-0.145, 0.104)	-0.011 (-0.164, 0.086)	-0.009 (-0.151, 0.086)	-0.008 (-0.148, 0.089)
F	-0.01 (-0.13, 0.067)	-0.006 (-0.117, 0.07)	-0.009 (-0.126, 0.063)	-0.009 (-0.126, 0.064)	-0.009 (-0.129, 0.063)	-0.011 (-0.13, 0.055)
Predator density						
CropDiv 5	**0.275 (0.015, 0.536)**	**0.245 (0.048, 0.476)**	0.09 (-0.058, 1.171)	-0.003 (-0.292, 0.269)	-0.016 (-0.299, 0.189)	0.001 (-0.24, 0.247)
CropDiv 10	0.398 (-0.097, 1.022)	0.258 (-0.202, 0.861)	0.087 (-0.403, 1.405)	-0.004 (-0.677, 0.488)	-0.016 (-0.622, 0.477)	0.002 (-0.454, 0.637)
CropDiv 15	0.2 (-0.423, 0.743)	0.221 (-0.414, 0.687)	0.084 (-0.497, 1.348)	-0.004 (-0.716, 0.489)	-0.016 (-0.655, 0.48)	0.001 (-0.521, 0.609)
CropDiv S5-S10	0.122 (-0.112, 0.486)	0.013 (-0.25, 0.385)	-0.003 (-0.345, 0.234)	-0.001 (-0.385, 0.219)	-0.001 (-0.323, 0.289)	-0.001 (-0.214, 0.39)
CropDiv S5-S15	-0.075 (-0.438, 0.207)	-0.024 (-0.462, 0.211)	-0.006 (-0.439, 0.177)	-0.001 (-0.424, 0.22)	-0.001 (-0.356, 0.291)	-0.001 (-0.281, 0.361)
CropDiv S10-S15	**-0.198 (-0.559, -0.046)**	-0.037 (-0.461, 0.075)	-0.004 (-0.327, 0.175)	0.001 (-0.283, 0.244)	-0.001 (-0.275, 0.245)	-0.001 (-0.306, 0.21)
SNH	0.093 (-0.04, 0.343)	0.127 (-0.023, 0.385)	0.046 (-0.113, 0.348)	0.011 (-0.247, 0.334)	0.024 (-0.168, 0.32)	0.042 (-0.118, 0.354)
CropDiv:SNH	-0.0025 (-0.16, 0.125)	0.0104 (-0.197, 0.315)	-0.0039 (-0.398, 0.26)	0.0071 (-0.137, 0.61)	0.0074 (-0.073, 0.384)	0.0025 (-0.183, 0.392)
S5-10	**0.818 (0.502, 1.135)**	**0.864 (0.561, 1.167)**	**0.872 (0.573, 1.171)**	**0.87 (0.571, 1.169)**	**0.87 (0.571, 1.168)**	**0.869 (0.57, 1.168)**
S5-15	**0.699 (0.359, 1.038)**	**0.715 (0.375, 1.054)**	**0.721 (0.383, 1.059)**	**0.717 (0.379, 1.054)**	**0.715 (0.378, 1.052)**	**0.715 (0.378, 1.052)**
S10-15	-0.12 (-0.401, 0.161)	-0.149 (-0.42, 0.122)	-0.151 (-0.419, 0.117)	-0.153 (-0.421, 0.114)	-0.154 (-0.422, 0.113)	-0.154 (-0.393, 0.116)
B	0.031 (-0.133, 0.335)	0.031 (-0.132, 0.333)	0.029 (-0.138, 0.327)	0.028 (-0.137, 0.327)	0.028 (-0.137, 0.327)	0.029 (-0.137, 0.328)
A	**0.253 (0.147, 0.359)**	**0.27 (0.166, 0.374)**	**0.282 (0.177, 0.387)**	**0.278 (0.174, 0.383)**	**0.277 (0.173, 0.381)**	**0.277 (0.172, 0.381)**
SOC	0.048 (-0.164, 0.432)	0.051 (-0.158, 0.462)	0.063 (-0.177, 0.539)	0.041 (-0.219, 0.497)	0.039 (-0.216, 0.484)	0.042 (-0.213, 0.488)
F	-0.011 (-0.271, 0.183)	-0.012 (-0.276, 0.177)	-0.015 (-0.282, 0.17)	-0.014 (-0.283, 0.169)	-0.015 (-0.283, 0.169)	-0.014 (-0.283, 0.169)

Response	100	250	500	1000	2000	3000
Parasitoid density						
CropDiv	0.042 (-0.335, 0.648)	0.013 (-0.406, 0.513)	-0.115 (-0.526, 0.189)	0.149 (-0.169, 0.873)	**0.578** **(0.173, 1.056)**	**0.348** **(0.048, 0.893)**
SNH	0.001 (-0.495, 0.502)	-0.015 (-0.582, 0.456)	**-0.498** **(-1.21, -0.148)**	-0.1 (-0.944, 0.4)	0.018 (-0.348, 0.455)	-0.031 (-0.557, 0.342)
CropDiv:SNH	NA	-0.0134 (-1.182, 0.157)	**-0.819** **(-2.012, -0.671)**	0.01 (-0.46, 1.077)	0.038 (-0.083, 0.602)	0.013 (-0.271, 0.69)
B	0.07 (-0.226, 0.669)	0.068 (-0.227, 0.668)	0.059 (-0.12, 0.532)	0.069 (-0.229, 0.669)	0.0557 (-0.254, 0.649)	0.062 (-0.243, 0.655)
A	**0.651** **(0.361, 0.942)**	**0.648** **(0.359, 0.937)**	**0.639** **(0.43, 0.848)**	**0.699** **(0.376, 1.023)**	**0.794** **(0.454, 1.133)**	**0.697** **(0.392, 1.001)**
SOC	0.22 (-0.347, 1.49)	0.168 (-0.357, 1.316)	0.156 (-0.125, 1.064)	0.225 (-0.326, 1.475)	0.521 (-0.017, 1.666)	0.264 (-0.249, 1.46)
F	-0.24 (-1.423, 0.286)	-0.235 (-1.423, 0.296)	-0.257 (-1.19, 0.025)	-0.274 (-1.486, 0.264)	-0.346 (-1.481, 0.16)	-0.277 (-1.471, 0.25)

Fixed effect abbreviations: A = Aphid density, B = Bird exclusion (birds excluded yes/no), CropDiv = Crop diversity, F = Nitrogen fertilization (fertilizer applied yes/no), SNH = Proportion of seminatural habitat, SOC = Soil organic carbon content (soil organic carbon content low/high), S = Survey interval (5 = day 0 to 5, 10 = days 5 to 10, 15 = days 10 to 15), CropDiv:S = Interaction Crop diversity x Survey interval e.g. CropDiv:S5-S10 = difference in CropDiv effects between survey interval 5 (days 0 to 5) and 10 (days 5 to 10), CropDiv:SNH = interaction crop diversity x proportion of seminatural habitat.

* Fertilization and SOC are included due to the nature of the experimental design and analysis, yet not further developed in this paper.

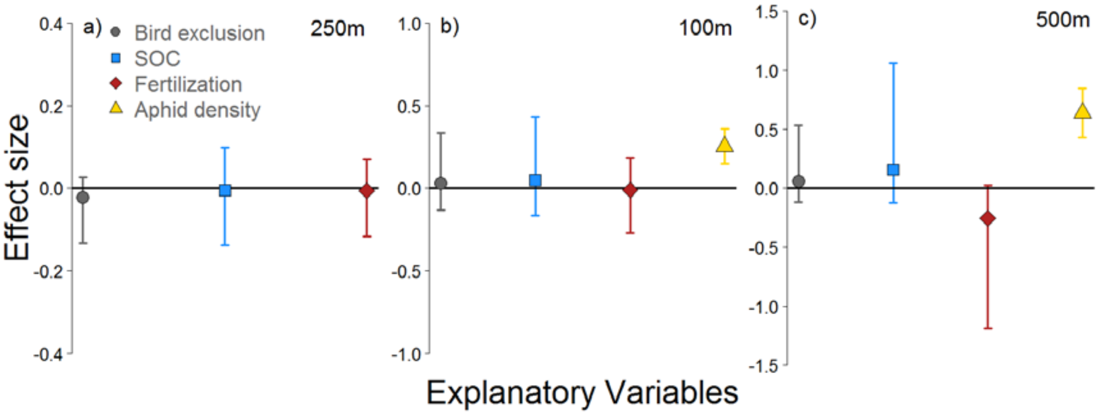


Figure III.S1 Model-averaged effect sizes and 95% confidence intervals explaining a) biological control, b) predator and c) parasitoid density (based on day 15 only). Shown are effects of the predictor variable bird exclusion (negative/positive effect sizes indicate respective decreases/increases in the response with birds present), and the covariates soil organic carbon (SOC, high/low), fertilization (yes/no) and aphid included in models with Δ AICc < 7. Confidence intervals not including zero (horizontal line) indicate effect sizes of large importance. Plotted for most predictive scales (highest R^2 values).

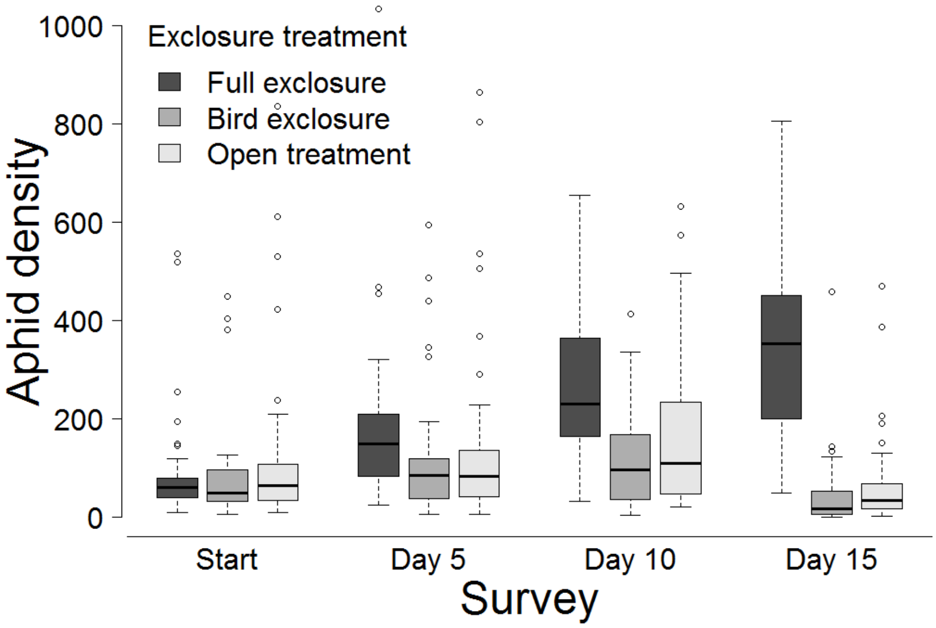


Figure III.S2 Effects of natural enemy exclusion and treatment duration on aphid densities on day zero (start of experiment), day 5, 10, and 15. The broad line, and the lower and upper bounds of each box correspond to median, 25% and 75% quartiles, respectively; open circles represent potential outliers. Initial aphid densities in exclusion treatments were similar (generalized linear mixed effects model of initial aphid densities (Day 0) as function of cage treatment; parameter estimates (95% confidence intervals) 'Full Exclosure' vs. 'Bird Exclosure': -0.105 (-0.451; 0.241); 'Full Exclosure' vs. 'Open Treatment': 0.0483 (-0.298; 0.394); 'Bird Exclosure' vs. 'Open Treatment': 0.154 (-0.193; 0.5)).

Chapter IV

Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes

Crop diversification has been proposed as farm management tool that could mitigate the externalities of conventional farming while reducing productivity-biodiversity trade-offs. Yet evidence for the acclaimed biodiversity benefits of landscape-level crop diversity is ambiguous. Effects may strongly depend on spatial scale and the level of landscape heterogeneity (e.g. overall habitat diversity). At the same time, contrasting within-taxon responses obscure benefits to specific functional groups (i.e. species with shared characteristics or requirements) if studied at the community level. The objectives of this study were to 1) disentangle the relative effects of crop diversity and landscape heterogeneity on avian species richness across five spatial scales ranging from 250 to 3000 m radii around focal winter wheat fields; and 2) assess whether functional groups (feeding guild, conservation status, habitat preference, nesting behaviour) determine the strength and direction of responses to crop diversity and landscape heterogeneity. In central Germany, 14 landscapes were selected along independent gradients of crop diversity (annual arable crops) and landscape heterogeneity. Bird species richness in each landscape was estimated using four point counts throughout the breeding season. We found no effects of landscape-level crop diversity on bird richness and functional groups. Instead, landscape heterogeneity was strongly associated with increased total bird richness across all spatial scales. In particular, insect-feeding and non-farmland birds were favoured in heterogeneous landscapes, as were species not classified as endangered or vulnerable on the regional Red List. Crop-nesting farmland birds, however, were less species-rich in these landscapes. Accordingly, crop diversification may be less suitable for conserving avian diversity and associated ecosystem services (e.g. biological pest control), although confounding interactions with management intensity need yet to be confirmed. In contrast, enhancement of landscape heterogeneity by increasing perennial habitat diversity, reducing field sizes and the amount of cropland has the potential to benefit overall bird richness. Specialist farmland birds, however, may require more targeted management approaches.

IV.1 Introduction

Agrochemical inputs, intensive crop rotations and removal of non-crop habitats directly and indirectly affect resource availability and habitat diversity in agroecosystems. As a result, biodiversity and ecosystem services decline (Benton *et al.*, 2003; Boesing *et al.*, 2017). Agricultural extensification (the use of less intensive farming methods) could mitigate these trends. To date, biodiversity conservation efforts primarily focus on extensification measures that facilitate the often-pronounced relationship between taxonomic biodiversity and the amount and diversity of non-crop habitats. However, apparent biodiversity-productivity trade-offs lower the profitability and uptake of extensification approaches such as flower strip plantings or set-asides, which often require arable land to be taken out of production (Khoury *et al.*, 2014).

Crop diversification (i.e. increasing the number and evenness of crops grown within a given landscape) has been proposed as an alternative extensification strategy that could reduce the negative effects of conventional farming without jeopardizing productivity goals (Fahrig *et al.*, 2011). Like non-crop habitat diversity, landscape-level crop diversity can play a vital role in sustaining biodiversity and ecosystem services. By providing a variety of complementary resources and habitats in space and time, more species with multiple and seasonal extended resource requirements or different niches are able to persist (complementation or niche differentiation effects) (Fahrig *et al.*, 2011; Kremen & Miles, 2012; Rusch *et al.*, 2013; Palmu *et al.*, 2014; Schellhorn *et al.*, 2015; Redlich *et al.*, 2018). These additional resources are particularly relevant in intensively farmed landscapes, where non-crop elements such as seminatural habitats are often deteriorated beyond functional importance (Tscharntke *et al.*, 2016).

Yet evidence for the benefits of landscape-level crop diversity (hereafter 'crop diversity') is ambiguous, especially with respect to birds. Birds, in particular farmland birds, contribute a range of essential ecosystem services such as pest control (herbivore and weed seed removal, (Mäntylä *et al.*, 2011; Boesing *et al.*, 2017)) and nutrient cycling (Whelan *et al.*, 2008). The composition of bird assemblages relates to the quality, structural diversity, disturbance level and food availability of cropping systems at local and landscape scales, thereby giving insights into the state of plant, insect and vertebrate diversity as a whole (Gregory *et al.*, 2005). Yet previous findings showcase a range of very context-specific and opposing effects (Firbank *et al.*, 2008; Lindsay *et al.*, 2013; Fahrig *et al.*, 2015; Hiron *et al.*, 2015; Josefsson *et al.*, 2017).

Crop diversity benefits may vary depending on the spatial scale considered (Gabriel *et al.*, 2010; Miguet *et al.*, 2013; Jackson & Fahrig, 2015; Jeliazkov *et al.*, 2016), and can be confounded by or interact with landscape heterogeneity (Tscharntke *et al.*, 2012; Palmu *et al.*, 2014; Josefsson *et al.*, 2017). Here, we define landscape heterogeneity as an array of strongly interrelated components of configuration (mean patch size) or composition (perennial habitat diversity, seminatural habitat cover) that do not relate to the type of crops grown within the landscape. Choosing an inadequate spatial scale or missing correlations with landscape heterogeneity aspects could therefore result in false positive, negative or absent effects of crop diversity. At the same time, crop diversity effects may not equally apply to all bird species, owing to different resource, habitat and nesting preferences of specific functional groups (i.e. species with shared characteristics or requirements), so that individual responses could be masked in whole community analysis (Filippi-Codaccioni *et al.*, 2010; Ndang'ang'a *et al.*, 2013a; Chiron *et al.*, 2014; Hiron *et al.*, 2015). Whether effects are found may also depend on the choice of crop diversity index (i.e. which crops are included or whether they are grouped) (Josefsson *et al.*, 2017). As most studies have been restricted to crop diversity estimates based on a limited number of crops (Herzon & O'Hara, 2007; Gottschalk *et al.*, 2010; Wretenberg *et al.*, 2010; Miguet *et al.*, 2013), single-species responses (Everaars *et al.*, 2014; Sauerbrei *et al.*, 2014), subsets of the whole community (e.g. farmland birds, (Hiron *et al.*, 2015; Josefsson *et al.*, 2017)), or one spatial scale (Wretenberg *et al.*, 2010; Fahrig *et al.*, 2015), this could explain some of the contrasting crop-bird diversity patterns observed.

In this study, we explore the relationship between bird richness and crop diversity, while uncovering factors mediating or limiting benefits for bird communities in agroecosystems. To disentangle crop diversity effects from landscape heterogeneity, 14 sites were selected along two independent gradients of crop diversity and perennial habitat diversity (here used as proxy for landscape heterogeneity). At each site, landscape variables were calculated for five spatial scales (250m, 500m, 1000m, 2000m, 3000m). Opposed to previous studies, we use a crop functional diversity index based on all arable crops grown within the different landscapes. Using bird surveys, we distinguished between influences on the whole bird community, and four functional groups (defined by 'feeding guild', 'habitat preference', 'nesting behaviour' and 'conservation status'), while posing four hypotheses: First, we expected a positive association between crop diversification and overall bird species richness (complementation or niche differentiation effects, (Fahrig *et al.*, 2011)). Second, we anticipated varying responses of different functional groups such as endangered vs. non-threatened species (Chiron *et al.*, 2014). Third, we tested the hypothesis that crop diversity effects on the whole community and functional groups depend on the level of landscape heterogeneity (intermediate landscape complexity hypothesis (Tscharntke *et al.*, 2012)) or, fourth, the spatial scale considered (Jeliazkov *et al.*, 2016).

The landscape-level diversity of annual arable crops is associated with high spatial and temporal variability. Crop diversity therefore represents a flexible and adaptable component of a farm, which increases its utility as targeted biodiversity enhancement measure (Aguilar *et al.*, 2015). Here, we shed new light on the possibilities and context-dependencies of crop diversity as conservation tool by considering functional group identity, landscape context and spatial scale.

IV.2 Material and Methods

IV.2.1 Study region and field selection

Fieldwork was carried out in 2014 in a c. 25 km by 40 km area near Würzburg /Germany (49°47` N, 9°57` E). The intensively cultivated region is dominated by cereals, sugar beets, maize and oil crops, and home to a number of red-listed bird species (Bayerisches Landesamt für Umwelt 2016). Here, 14 focal winter wheat fields were selected along gradients of crop diversity at various scales. Focal fields were at least 1000 m apart (range 1012 m to 2560 m) and selected to have structurally similar field margins (simple grass margins).

IV.2.2 Crop diversity

Resource complementation effects rely on the presence of functionally different plant types (Fahrig *et al.*, 2011; Josefsson *et al.*, 2017). Indices estimating diversity based on a large number of crops with similar structure, resources and ecological functions (e.g. wheat, barley, triticale) may therefore overestimate the functional diversity. However, the assignment of specific functions to crops strongly depends on preferences of individual study organisms, which makes this approach particularly difficult in whole community studies. In addition, the inclusion of only a subset of main crops such as cereals, maize and rotational grasslands - as done in previous studies (Herzon & O'Hara, 2007; Gottschalk *et al.*, 2010; Wretenberg *et al.*, 2010; Miguet *et al.*, 2013) – may mask important crop diversity effects of less prominent functional crop groups. Based on these considerations, we therefore used all arable crops grown within the study region to create 12 crop categories (Table IV.1) according to the structural similarity and relatedness of the crops (Eurostat, 2012; Josefsson *et al.*, 2017). Landscape-level crop diversity ("CropDiv") was then calculated as Shannon Wiener index in the 'vegan' package in R (Oksanen *et al.*, 2015) for five spatial scales (250, 500, 1000, 2000 and 3000 m radius around a centroid placed halfway between the two bird observation points, Table IV.S1). Scales were chosen based on known home ranges of birds, and previous research. The regional agricultural land-use data for 2014 was obtained from the Bavarian State Ministry of Nutrition, Agriculture and Forestry. To assess the risk of underestimating crop diversity using this grouping approach, all analyses were repeated using crop species diversity based on 58 arable crops. The results did not change, but model fit was lower. This supports the use of crop functional rather than crop species diversity (Josefsson *et al.*, 2017).

Table VI.1 Description of landscape parameters and species richness variables. Summary statistics of landscape parameters and species richness variables. For landscape parameters crop diversity ("CropDiv") and perennial habitat diversity (LandHet, the proxy for landscape heterogeneity) summary statistics are averaged across all study sites (n=14) and spatial scales (n=5). For total and functional group richness, values are averaged across study sites.

	Min	1st Q	Median	Mean	3rd Q	Max	Description
Landscape parameters							
CropDiv[a]	0	0.84	1.05	1.01	1.21	1.48	Shannon index calculated from the proportional cover of twelve crop types: cereals (excluding grain maize), 1- or 2-year old fallows, flowers and ornamental plants, temporary grassland and green fodder (green maize), legumes, maize, oilseed and fibre crops (excluding rape), rape and turnips, root crops, sunflowers, vegetables, other industrial crops
LandHet[a]	0.05	0.44	0.71	0.68	0.9	1.32	Due to the high correlation of variables representing aspects of landscape heterogeneity (see text), perennial habitat diversity was used as proxy for the level of heterogeneity in the surrounding landscapes. LandHet was calculated as Shannon index using the proportional cover of six perennial non-crop habitat types: forest, seminatural habitat (orchard meadows, hedgerows, forest edges, field margins, old fallows), settlement, water, perennial crops, extensive permanent grassland. Landscapes with high LandHet also had smaller field sizes, less cropland and more seminatural habitat
Species richness[b]							
Total (63)	15	20	22.5	22.4	25.7	31	Total number of bird species in landscapes. Data obtained from point counts, excluding flocks of birds passing fields.
Feeding guild							
Insectivore (35)	8.0	14.2	15.5	15.6	17	23	Insect content of diet >60% (including macroinvertebrates)
Granivore (12)	1	1.3	2.5	2.3	3	4	Seed and plant content of diet >60%
Carnivore (7)	1	2	2	2.2	2	5	Vertebrate content of diet ≥60%
Omnivore (9)	1	1	2	2.4	3	4	Mixed plant and invertebrate diet
Conservation status							
Least concern (42)	10	15.2	17	16.8	19	21	Bird species with stable population sizes
Vulnerable (10)	1	2	2	2.9	3	6	Bird species listed as vulnerable in the Bavarian Red List
Endangered (11)	1	2	3	2.9	3.8	5	Bird species listed as endangered, critically endangered, regionally extinct, very rare or geographically restricted
Habitat preference							
Farmland (25)	5	7	9	9.2	11	14	Nesting and/or foraging predominantly in cropland
Non-farmland (38)	6	12	13	13.1	15.8	19	Nesting and/or foraging predominantly in non-crop habitat
Nesting behaviour							
Crop nester (8)	1	2	2	2.5	3	5	Subset of farmland birds nesting in cropland
Non-crop nester (17)	3	4.5	6	6.6	7.8	12	Subset of farmland birds nesting in non-crop habitat

[a] For summary statistics of individual spatial scales (250, 500, 1000, 2000 and 3000m) see S1 Table

[b] Total number of bird species across all study sites for the whole bird community and individual functional groups shown in brackets

IV.2.3 Landscape heterogeneity

In contrast to CropDiv, other influential landscape aspects such as the diversity of non-crop perennial habitats, arable field size, the proportion of cropland and seminatural habitat cover can be viewed as indicators of landscape heterogeneity not directly related to the type of crop grown. These aspects of landscape composition and configuration can potentially confound crop diversity effects (Fahrig *et al.*, 2011). During field selection, correlations with CropDiv were therefore kept to a minimum (Table IV.S1). However, as these variables were highly correlated amongst themselves (Table IV.S1), only perennial habitat diversity (hereafter "LandHet", correlation with CropDiv r=0.05 – 0.4, Table IV.S1) was used in our analysis as proxy for the overall level of landscape heterogeneity. Accordingly, heterogeneous landscapes had a high perennial habitat diversity, a high proportion of seminatural habitat, low cropland cover and small arable field sizes. The indicator variable LandHet was calculated as Shannon Wiener index of six perennial habitat types (Table IV.1), which were digitized in ArcMap v. 10 (ESRI 2011) using official digital topological maps ATKIS DTK 25 (Bayerische Vermessungsverwaltung).

IV.2.4 Bird observations

Birds were surveyed four times between May and July 2014 next to the focal winter wheat fields. The observation period was chosen to coincide with the major breeding season of birds in Germany. Each survey comprised two 10-minute point counts, one located in the open grass field margin, the other close to the nearest non-crop habitat, the type of which was also recorded (shrubs, forest, other). Distance between field margins and nearest non-crop habitat ranged between 20 to 100 m, the midpoint acted as centroid for landscape calculations. Fields were visited from 4:30 am to 9 am in the morning, or 5 pm to 8:30 pm in the evening. The order and time of visits was randomized. All birds seen or heard within a radius of 100 m were recorded (Bibby *et al.*, 1992). No distinctions were made between birds breeding or foraging. Surveys were not conducted during windy or rainy weather. All observations were done by a single observer (B.W.), and care was taken not to double-count individual birds.

Bird richness was then based on all species recorded in each landscape during the four visits, with field and non-crop point counts pooled per site. Groups of flocking birds crossing the fields were not included in species richness calculations. Observed and rarefied species richness (estimated in the 'vegan' package in R) were highly correlated (Pearson's $r = 0.93$), suggesting that sampling effort was sufficient. Bird species richness was further partitioned into functional groups (Table IV.1, Table IV.S2) based on overall 'habitat preference' and 'feeding guild' (Henderson *et al.*, 2009; Chiron *et al.*, 2014; EBBC, 2015). Birds primarily foraging in cropland may also vary in their sensitivity to crop and non-crop components of agroecosystems owing to their 'nesting behaviour' (Hiron *et al.*, 2015; Josefsson *et al.*, 2017). We consequently used the farmland bird subset to distinguish between crop and non-crop nesting species. Finally, we assessed the responsiveness of endangered and vulnerable species in comparison to those with least conservation concern ('conservation status' as indicated by the regional Red List assessment (Bayerisches Landesamt für Umwelt, 2016)).

IV.2.5 Statistical analysis

The effects of crop diversity (CropDiv) and landscape heterogeneity (LandHet) on bird richness were analyzed by applying linear models (total richness) and linear mixed effects models (richness of functional groups; R package 'nlme'; (Pinheiro *et al.*, 2016)) R Statistical Software v.3.2.2 (R Development Team, 2016). Separate models were fitted for each of the five spatial scales. The scale with the strongest landscape effect was then determined by comparing AICc values of full models. For total richness, fixed factors for each scale-specific model were CropDiv, LandHet and their interaction. To identify guild-specific differences in response, the models assessing effects on species richness of the functional groups ('Func') feeding guild, conservation status, habitat preference and nesting behaviour also included the interactions Func x CropDiv and Func x LandHet. Sample size for functional group models varied depending on the number of functional guilds per group (e.g. four feeding guilds in all but one landscapes; Table IV.2). In these models, 'study site' was entered as random term, and variance structures (varIdent) were added for the functional groups feeding guild, conservation status and nesting behavior, to account for variance heterogeneity. All models were fitted using Gaussian distribution as graphical validation of normality and homogeneity of residuals suggested that assumptions for linear models were met. In addition, the complexity of our models and the need to include variance structures justifies the use of Gaussian over Poisson distribution despite the count nature of the data (Warton *et al.*, 2016). We did not observe significant spatial autocorrelation of residuals (Moran's I test in R package 'ape', all p-values > 0.096 (Paradis *et al.*, 2004)). Both landscape variables were z-standardized (R package 'base', version 3.2.2) to reduce multicollinearity and enhance interpretability of main effects. Model simplification was performed using likelihood ratio-based manual stepwise deletion of non-significant interaction terms. We assessed the significance of fixed effects using F-tests for linear models (total species richness) and Wald chi-square tests for linear mixed effects models with random terms (species richness of functional groups).

In the presence of marginal or significant interactions, we used post hoc multiple comparisons of slopes with manually defined contrast matrices (R package 'multcomp', (Hothorn *et al.*, 2008)) to determine whether species richness responses of individual functional guilds differed from zero. For this purpose, p-values were adjusted for the False Discovery Rate (Benjamini & Yekutieli, 2001). We repeated the functional groups analyses by excluding guilds with an average of less than three species per field. As the results were qualitatively the same, we thereby confirmed that findings were not affected by the imbalance between highly abundant and rare groups. In addition, this approach highlighted the importance of further investigating individual guild responses in the presence of marginal interactions between functional groups and landscape variables.

Model fit was assessed using adjusted R^2 for linear models (total species richness) and marginal R^2 (considering fixed effects only) for linear mixed models in functional group analyses (function 'r.squaredGLMM' in R 'MuMIn' package (Nakagawa & Schielzeth, 2013)).

IV.3 Results

During four field visits, we observed 63 bird species with a summed total abundance of 1520 individuals. Bird richness varied significantly with the functional group considered (Tables IV.1 & IV.2, Table IV.S1). Insect-feeding and non-farmland bird species were most common, while 17 out of 25 species of farmland birds were non-crop nesters. Although non-threatened birds were most prominent, species listed as endangered and vulnerable on the Bavarian Red List 2016 were recorded in all landscapes, with an average of six species per site encountered during the four visits. The endangered skylark *Alauda arvensis* was the most abundant species (17.8% of observations) and occurred at all sites. The red-listed Eurasian wryneck *Jynx torquilla* and the grey partridge *Perdix perdix* were recorded only once, thereby each accounting for only c. 0.07% of all observations (Table IV.S2).

IV.3.1 Landscape and scale effects on bird communities

Crop diversity did not affect bird communities regardless of the scale or functional group considered (Figure IV.1, Table IV.2). In contrast, landscape heterogeneity enhanced several aspects of bird richness considered in this study. Interactions between crop diversity and landscape heterogeneity were not observed.

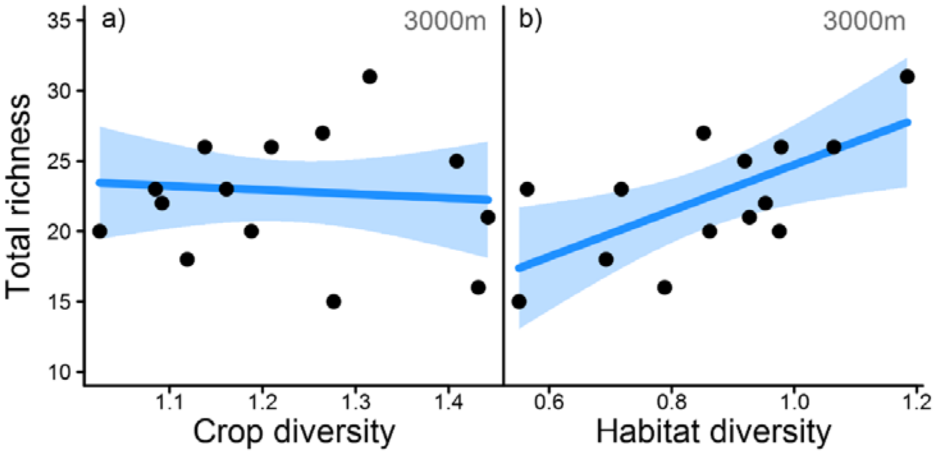


Figure IV.1 Landscape effects on total bird richness. Effects of a) landscape-level crop diversity (CropDiv) and b) perennial habitat diversity (LandHet, proxy for overall landscape heterogeneity) on total species richness. Exemplified for landscape effects at the 3000 m scale (lowest AICc value) with predicted values for each study site (n=14). Regression line and 95% confidence intervals shown.

Table IV.2 Effects of crop diversity and landscape heterogeneity on bird richness. Linear models relating total and functional group bird richness to crop diversity (CropDiv), perennial habitat diversity (LandHet, the proxy for landscape heterogeneity) and functional group (Func, only for functional groups models). Two-way interactions between functional group and landscape variables were included in full models yet removed during backwards stepwise model selection if non-significant. The random effect 'Study site' was added in functional group models to account for non-independence of samples within study sites. Analysis of nesting behaviour was limited to the farmland bird subset (25 out of 63 species). Significant p-values <0.05 are indicated in bold. Model fit was determined with adjusted R2 (total richness) and marginal R2 (richness of functional groups) using the function 'r.squaredGLMM' ('MuMIn' package). Sample sizes (n) varied depending on functional group considered. Significance of fixed effects assessed using F-tests (linear models for total species richness) and Wald chi-square tests (linear mixed effects models with random terms for species richness of functional groups).

Predictor	Community richness (*n*=14)				Feeding guild (*n*=55)			Conservation status (*n*=41)			Habitat preference (*n*=28)			Farmland nesters (*n*=28)		
Scale	*nDF*	*dDF*	*F*	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*
250m	R^2=0.3				R^2=0.98			R^2=0.92			R^2=0.35			R^2=0.91		
Func	*NA*	*NA*	*NA*	*NA*	3	223.8	**<0.001**	2	335.2	**<0.001**	1	10.08	**0.002**	1	27.12	**<0.001**
CropDiv	1	11	1.53	0.243	1	0.39	0.535	1	1.43	0.232	1	1.08	0.298	1	1.37	0.242
LandHet	1	11	5.78	**0.035**	1	1.15	0.284	1	0.14	0.706	1	4.11	**0.043**	1	5.76	**0.016**
Func x LandHet	*NA*	*NA*	*NA*	*NA*	3	14.25	**0.003**	2	8.84	**0.012**	-	-	-	1	3.54	0.06
500m	R^2=0.45				R^2=0.98			R^2=0.91			R^2=0.45			R^2=0.89		
Func	*NA*	*NA*	*NA*	*NA*	3	482.4	**<0.001**	2	450.3	**<0.001**	1	15.83	**0.001**	1	27.12	**<0.001**
CropDiv	1	11	1.06	0.325	1	0.03	0.859	1	1.05	0.305	1	0.88	0.349	1	1.06	0.304
LandHet	1	11	6	**0.032**	1	3.64	0.056	1	0.01	0.932	1	0.01	0.987	1	7.89	**0.005**
Func x LandHet	*NA*	*NA*	*NA*	*NA*	3	27.6	**<0.001**	2	5.73	0.057	1	5.31	**0.021**	1	3.04	0.081
1000m	R^2=0.42				R^2=0.97			R^2=0.91			R^2=0.5			R^2=0.9		
Func	*NA*	*NA*	*NA*	*NA*	3	367.2	**<0.001**	2	301.3	**<0.001**	1	12.98	**<0.001**	1	24.15	**<0.001**
CropDiv	1	11	1.85	0.201	1	0.78	0.377	1	1.62	0.204	1	1.27	0.261	1	2.56	0.11
LandHet	1	11	7.73	**0.018**	1	1.67	0.197	1	0.01	0.945	1	0.01	0.983	1	3.94	**0.047**
Func x LandHet	*NA*	*NA*	*NA*	*NA*	3	32.87	**<0.001**	2	5.27	0.072	1	5.37	**0.02**	-	-	-

Predictor	Community richness (*n*=14)				Feeding guild (*n*=55)			Conservation status (*n*=41)			Habitat preference (*n*=28)			Farmland nesters (*n*=28)		
Scale	*nDF*	*dDF*	*F*	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*	*DF*	χ^2	*p*
2000m	R^2=0.43				R^2=0.98			R^2=0.96			R^2=0.47			R^2=0.89		
Func	*NA*	*NA*	*NA*	*NA*	3	190.7	**<0.001**	2	259.4	**<0.001**	1	12.45	**<0.001**	1	24.15	**<0.001**
CropDiv	1	11	1.81	0.206	1	0.52	0.47	1	0.05	0.827	1	1.18	0.276	1	1.53	0.216
LandHet	1	11	10.17	**0.009**	1	2.07	0.15	1	1.93	0.165	1	0.14	0.706	1	2.36	0.125
Func x LandHet	*NA*	*NA*	*NA*	*NA*	3	37.63	**<0.001**	-	-	-	1	4.21	**0.04**	-	-	-
3000m	R^2=0.34				R^2=0.97			R^2=0.97			R^2=0.41			R^2=0.85		
Func	*NA*	*NA*	*NA*	*NA*	3	88.74	**<0.001**	2	248.3	**<0.001**	1	12.31	**<0.001**	1	24.15	**<0.001**
CropDiv	1	11	0.15	0.707	1	0.01	0.968	1	1.23	0.267	1	0.11	0.739	1	0.03	0.874
LandHet	1	11	8.55	**0.014**	1	1.44	0.23	1	1.68	0.195	1	6.41	**0.011**	1	0.77	0.381
Func x LandHet	*NA*	*NA*	*NA*	*NA*	3	22.56	**<0.001**	-	-	-	-	-	-	-	-	-

Extensive landscapes offering a variety of non-crop and perennial habitats, smaller field sizes and lower cropland cover generally harboured the most diverse bird assemblages across all scales (Figure IV.1a, Table IV.2). This positive relationship between landscape heterogeneity and total species richness was driven by the response of dominant functional groups such as insectivores, non-farmland birds or species of least conservation concern (Figure IV.2, Table IV.2, Table IV.S3). Accordingly, birds preferentially feeding on arthropods were enhanced in extensive landscapes across multiple scales, although the remaining feeding guilds were unaffected (Figure IV.2a, Table IV.2, Table IV.S3). Non-threatened birds ('least concern' on the regional Red List) were facilitated by landscape heterogeneity at the 250 to 1000 m scale (Figure IV.2b, Table IV.2, Table IV.S3). Although functional group x LandHet interactions were only marginal on the larger scales, post hoc comparisons showed strong increases in the species richness of this dominant group, which was confirmed by single-guild analyses. Neither vulnerable nor endangered species showed similar responses. We also observed a positive influence of intermediate-scale landscape heterogeneity on non-farmland birds (500-2000 m scale, Figure IV.2c, Table IV.2, Table IV.S3). In contrast, the group of farmland specialists showed no benefits of landscape heterogeneity as a whole. However, the differentiation between nesting preference of farmland birds revealed strong reductions of crop-nesting birds at small scales (250-500m), whereas the positive relationship between non-crop nesters and landscape heterogeneity was non-significant due to high inter-field variability (Figure IV.2d, Table IV.2, Table IV.S3).

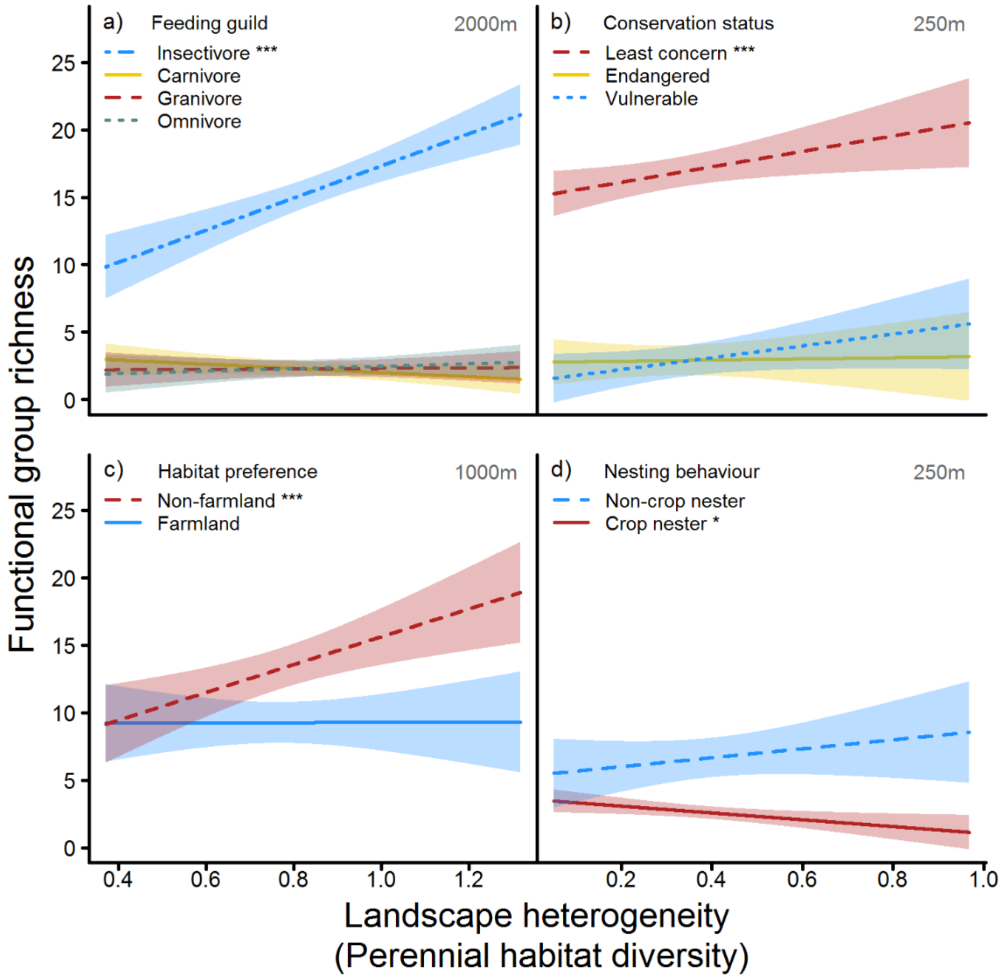


Figure IV.2 Habitat diversity effects on functional group richness. Effects of perennial habitat diversity (LandHet, proxy for overall landscape heterogeneity) on species richness of the functional groups a) feeding guild (2000m scale), b) conservation status (250m scale), c) habitat preference (1000m scale), and d) nesting behaviour (farmland bird subset, 250m) shown for scales with lowest AICc values. Slopes were tested against zero using contrast matrices with *p*-values adjusted for the False Discovery Rate ((Benjamini & Yekutieli, 2001) (Table IV.S3). Shown are fitted lines and 95% confidence intervals. Signifance levels: *** $p<0.001$, * $p<0.05$.

IV.4 Discussion

Our study assesses for the first time the individual and interactive effects of crop diversification and landscape heterogeneity on bird species richness and community structure across various spatial scales. We do this by disentangling crop diversity effects from the confounding influence of landscape heterogeneity variables such as perennial habitat diversity, mean field size, seminatural habitat and cropland cover.

Contrary to our hypothesis, we did not observe higher bird species richness in landscapes with diverse cropping systems, regardless of landscape context (low vs. high landscape heterogeneity), functional group or spatial scale considered. Therefore we cannot confirm previous findings that birds in general or functional groups such as non-crop breeding farmland species in particular benefit from crop functional diversity (Firbank *et al.*, 2008; Henderson *et al.*, 2009; Gottschalk *et al.*, 2010; Lindsay *et al.*, 2013; Miguet *et al.*, 2013; Ndang'ang'a *et al.*, 2013a; Josefsson *et al.*, 2017).

The spatial scale of a landscape often determines the outcome of landscape-biodiversity studies (Gabriel *et al.*, 2010; Jackson & Fahrig, 2015; Jeliazkov *et al.*, 2016; Redlich *et al.*, 2018). We overcome this limitation by including a range of local to landscape scales. We also accounted for different within-taxon responses that could mask total richness effects by distinguishing between different functional groups. For example, many farmland bird specialists show negative responses to diversification practices, as they rely on homogeneous systems with large fields and a large share of cereal crops, while non-farmland birds may benefit from the increase of non-crop resources (Filippi-Codaccioni *et al.*, 2010; Gabriel *et al.*, 2010; Chiron *et al.*, 2014; Santana *et al.*, 2017). In our study, however, farmland birds did not decline with crop diversification. These results are in line with studies that found no or very weak effects of crop diversity on farmland birds, when crop diversity measures were separated (uncorrelated) from other aspects of landscape heterogeneity.

The absence of crop diversity-biodiversity relationships in previous studies (Fahrig *et al.*, 2015; Hiron *et al.*, 2015; Santana *et al.*, 2017) suggests that birds may not rely on higher resource amount and continuity presumably provided by crop diversification. This could be the case, if birds do not require crop resources, or are otherwise able to compensate for reduced crop diversity by switching to non-crop resources. Crop diversity may therefore rise in importance in simplified landscapes, were non-crop resources are inadequate (Wretenberg *et al.*, 2010; Tscharntke *et al.*, 2016; Josefsson *et al.*, 2017). Despite being located in an intensively farmed area, non-crop habitat cover in our study region was relatively high, and fields small (average amount of seminatural habitat 18.6 ±1.5%, mean patch size 1.6±0.1 ha across study sites and all spatial scales). Accordingly, the mobile bird taxon may not have been as reliant on additional crop resources as in more simplified agroecosystems.

On the other hand, crop-specific pesticide and fertilizer applications, mowing, harvesting or grazing disturbance and other forms of agricultural management could obscure or counteract the benefits of increased resource availability (Jonsson *et al.*, 2012). For instance, a Swedish study reported increased ground beetle diversity with enhanced spatial crop diversity only after accounting for land-use management influences associated with tillage (Palmu *et al.*, 2014). Negative impacts of chemical intensification on bird diversity have also been reported on the farm scale, especially for ground-breeding farmland birds such as the skylark (Jeliazkov *et al.*, 2016). Specialist farmland birds are still the most endangered group of birds (Gregory *et al.*, 2005), and although some species respond positively to landscape and non-crop features, local reduction of agricultural intensification may be especially relevant for the conservation of crop-nesting birds (Guerrero et al., 2012). In our case, crop diversity showed a weak, positive trend with the frequency of insecticide application on the study field (Pearson's r=0.42, p-value=0.139). Higher rates of local insecticide application in landscapes with greater crop diversity could reduce invertebrate prey of insectivores, the most abundant dietary guild. If local application rates are comparable to farm-scale or regional values, this could explain the slight decline of overall bird richness with diversification on all spatial scales (Figure IV.1). As we do not have data on landscape-scale insecticide applications, this hypothesis warrants further investigation. However, apart from insecticide-driven reductions, crop-based invertebrate prey in diverse cropping systems may also be reduced due to enhanced insect-mediated pest control (Roschewitz et al., 2005; Rusch et al., 2013; Martin et al., 2016), although positive effects of landscape heterogeneity on predators do not always translate to lower prey availability(Tscharntke *et al.*, 2016). This may also affect the resource base and thereby the population size and richness of insect-feeding birds.

Lastly, specific crop types may be more important for avian communities, particularly farmland birds, than crop diversity per se. For example, cereals, pastures, set-asides and spring-sown crops have all been linked to changes in total and functional bird species richness, especially for farmland birds (Butler *et al.*, 2010; Gil-Tena *et al.*, 2015; Hiron *et al.*, 2015; Jeliazkov *et al.*, 2016; Josefsson *et al.*, 2017; Santana *et al.*, 2017). At the same time, the absolute observed difference in the number of crop types between low and high diversity landscapes was relatively small (difference of four crop types on average across all scales, Table IV.S1), although focal fields were selected to maximize the range of crop diversity. If additional crops were only grown in low proportions, or increases in crop diversity were driven by a more equal share of a selected number of main crops, then the benefits of crop diversification could be negligible (Fahrig *et al.*, 2015).

Either of these explanations of our non-significant findings are possible, yet other reasons are also worthwhile exploring. A taxon like birds, which covers a variety of functionally different and highly mobile species, may require larger spatial scales to detect benefits of crop diversity. For instance, prevalence of significant findings at the largest scale studied may indicate that more significant effects occurred outside the measured range (Jackson & Fahrig, 2015). Alternatively, weak effects of crop diversity (if present) may best be observed using a larger crop diversity gradient, and – due to high between-field variability- a larger sample size.

Opposed to crop diversity, the effects of landscape heterogeneity on bird communities were mainly positive. Our study used perennial habitat diversity as proxy for the overall level of landscape heterogeneity. Due to correlated landscape heterogeneity variables, we emphasize that it is impossible to disentangle the actual driver of the observed positive effects on bird diversity. They could either relate to 1) additional non-crop resources and habitats (resource complementation or niche differentiation (Fahrig *et al.*, 2011; Siriwardena *et al.*, 2012); 2) increased amounts of seminatural habitat such as field edges for foraging and nesting (Josefsson *et al.*, 2013); 3) smaller field sizes allowing for better access to adjacent non-crop habitats with abundant invertebrate prey (Lindsay *et al.*, 2013; Fahrig *et al.*, 2015; Jeliazkov *et al.*, 2016; Josefsson *et al.*, 2017); or 4) lower proportions of cropland, another indicator for heterogeneity and potentially reduced overall pesticide application

(Fahrig *et al.*, 2015; Jeliazkov *et al.*, 2016; Josefsson *et al.*, 2017). Drivers may vary depending on the functional group and scale considered, with scales of response (mainly 250 to 1000 m) comparing well with a previous study identifying the farm as the most relevant management scale for bird conservation purposes (Jeliazkov *et al.*, 2016).

Non-farmland birds include species that rely on forests, settlements or water bodies for nesting and foraging. They are apt to benefit from agricultural extensification and improved resource or habitat availability (Filippi-Codaccioni *et al.*, 2010; Gil-Tena *et al.*, 2015), as supported by our results at intermediate scales. The lack of enhancement at the 250 m scale may be due to the study design, which comprised conventionally managed focal fields with simple grass borders and low structural diversity at small spatial scales. Yet even these simple field boundaries and habitats may provide important foraging grounds with abundant prey resources for insectivores, particularly specialist farmland birds such as the skylark (Josefsson *et al.*, 2013; Gil-Tena *et al.*, 2015). Therefore, landscape heterogeneity may favour the diversity of this functional guild independent of the scale considered.

The increase in species richness of the group with the conservation status 'least concern' (250 to 1000 m scale) was likely driven by the positive response of insectivores and non-farmland birds, which made up almost 60% and 80% of 'least concern' species, respectively. However, the increase was less pronounced than in those guilds, possibly due to some common farmland species, that may have been negatively influenced by high landscape heterogeneity at the cost of cropland habitat and resources. Of the farmland birds, crop-nesters were the only functional guild with declining species richness in heterogeneous landscapes. However, this finding corroborates previous research highlighting the importance of homogeneous, open cropland for some crop-breeding farmland specialists (Hiron *et al.*, 2015), and the potentially detrimental role of field management intensity on this functional group (Guerrero et al., 2012).

The remaining functional groups did not show any specific responses to landscape heterogeneity. These groups, including non-insectivores, vulnerable or endangered species and non-crop nesters, may have very specific habitat or resource requirements not met with general diversification efforts (Bayerisches

Landesamt für Umwelt, 2016), and were rarely sampled in our study. For example, the Eurasian wryneck *Jynx torquilla* is more likely to benefit from targeted enhancement of high-value calcareous grasslands than from the extension of other seminatural habitat types (Bayerisches Landesamt für Umwelt, 2016).

IV.5 Conclusion

Three measures build the backbone of Greening, Pillar I of the European Common Agricultural Policy for the period 2015 – 2020 (CAP, EU Regulation No. 1307/2013), namely 1) retention of permanent grasslands, 2) ecological focus areas, and 3) crop diversification. All are intended to promote sustainable agriculture, biodiversity and ecosystem services, yet only the advantages of grasslands and non-crop habitats have been thoroughly studied. In support of Greening measure one and two, our study confirms that avian diversity, particularly non-farmland species and insectivores, can be enhanced by landscape heterogeneity (Fahrig *et al.*, 2011; Hiron *et al.*, 2015; Boesing *et al.*, 2017). We did not find, however, any benefits of landscape-level crop diversity for bird richness in intensively managed winter wheat systems, in contrast to studies on other taxa (e.g. Carabidae, (Palmu *et al.*, 2014)). Nevertheless, benefits may not only depend on scale, landscape context and functional groups, but also management intensity gradients or interspecific interactions with other agricultural species. This research avenue warrants further investigation. In general, we show that heterogeneity of agricultural landscapes and diversification of non-crop habitats directly benefit overall bird diversity, in addition to targeted, potentially field-based conservation measures aimed at increasing specific nesting and food resources of endangered specialist species.

IV.6 Supplement

Table IV.S1 Description of crop diversity and perennial habitat diversity. Summary statistics of crop diversity (CropDiv) and perennial habitat diversity (LandHet, the proxy for non-crop landscape heterogeneity) for different spatial scales. Shown are also the correlation coefficients (Pearson's r) of CropDiv and LandHet with the proportion of cropland (r crop), seminatural habitat cover (r SNH, including margins along linear elements such as roads and rivers) and average field size (r field). For CropDiv, the average number of crop types (and range) at each spatial scale are listed.

Scale	Min	1st Q	Median	Mean	3rd Q	Max	Average crop types	*r* LandHet	*r* crop	*r* SNH	*r* field
CropDiv											
250	0	0.513	0.67	0.686	0.888	1.239	3.3 (1-5)	0.4	-0.12	0.06	-0.58
500	0.5	0.698	0.914	0.915	1.021	1.442	5 (2-8)	0.22	-0.05	-0.24	-0.54
1000	0.74	0.862	1.037	1.056	1.223	1.443	5.4 (2-8)	-0.2	0.32	-0.41	-0.18
2000	0.984	1.056	1.184	1.2	1.332	1.483	8.8 (6-10)	0.05	0.02	-0.35	-0.04
3000	1.025	1.124	1.199	1.225	1.305	1.442	9.4 (8-11)	0.14	0.16	-0.28	-0.24
All scales	0	0.842	1.055	1.016	1.209	1.483	6.38 (1-11)	-	-	-	-
LandHet											
250	0.052	0.228	0.364	0.396	0.574	0.967	-	-	-0.82	0.53	-0.56
500	0.14	0.417	0.53	0.554	0.752	0.89	-	-	-0.92	0.8	-0.5
1000	0.371	0.614	0.727	0.764	0.89	1.319	-	-	-0.93	0.8	-0.5
2000	0.426	0.739	0.848	0.837	0.957	1.224	-	-	-0.96	0.82	-0.58
3000	0.551	0.735	0.89	0.859	0.97	1.185	-	-	-0.93	0.8	-0.7
All scales	0.052	0.436	0.709	0.682	0.899	1.319	-	-	-	-	-

Table IV.S2 Bird species classification. List of observed bird species with common name, habitat preference, feeding guild, Red List status (Germany and Bavaria), and total and relative abundance of species across 14 study sites.

Species	Common name	Feeding guild[1]	Conservation status[2]	Habitat preference[3]	Nesting behaviour[4]	Total abundance	Relative abundance
Acrocephalus scirpaceus	Eurasian reed-warbler	Insectivore	Least concern	Non-Farmland	Non-crop	5	0.33
Alauda arvensis	Eurasian skylark	Insectivore	Endangered	Farmland	**Crop**	271	17.83
Anas platyrhynchos	Mallard duck	Omnivore	Least concern	Non-Farmland	Non-crop	9	0.59
Apus apus	Common swift	Insectivore	Endangered	Farmland	**Non-crop**	9	0.59
Ardea cinerea	Grey heron	Carnivore	Vulnerable	Non-Farmland	Non-crop	2	0.13
Aythya fuligula	Tufted duck	Omnivore	Least concern	Non-Farmland	Non-crop	2	0.13
Buteo buteo	Common buzzard	Carnivore	Least concern	Non-Farmland	Non-crop	18	1.18
Carduelis cannabina	Common linnet	Granivore	Endangered	Farmland	**Non-crop**	2	0.13
Carduelis carduelis	European goldfinch	Granivore	Vulnerable	Farmland	**Non-crop**	2	0.13
Carduelis chloris	European greenfinch	Granivore	Least concern	Farmland	**Non-crop**	9	0.59
Certhia brachydactyla	Short-toed treecreeper	Insectivore	Least concern	Non-Farmland	Non-crop	1	0.07
Circus aeruginosus	Marsh harrier	Carnivore	Least concern	Farmland	**Crop**	1	0.07
Circus cyaneus	Hen harrier	Carnivore	Endangered	Non-Farmland	Non-crop	4	0.26
Circus pygargus	Montagu's harrier	Carnivore	Endangered	Farmland	**Crop**	5	0.33
Columba livia	Rock pigeon	Granivore	Least concern	Farmland	**Non-crop**	12	0.79
Columba palumbus	Common wood pigeon	Granivore	Least concern	Non-Farmland	Non-crop	92	6.05
Corvus corone	Carrion Crow	Omnivore	Least concern	Non-Farmland	Non-crop	2	0.13
Corvus frugilegus	Rook	Omnivore	Least concern	Farmland	**Non-crop**	45	2.96
Coturnix coturnix	Common quail	Granivore	Endangered	Farmland	**Crop**	3	0.20
Cuculus canorus	Common Cuckoo	Insectivore	Vulnerable	Non-Farmland	Non-crop	14	0.92
Delichon urbicum	Common house martin	Insectivore	Endangered	Farmland	**Non-crop**	70	4.61
Dendrocopos major	Great spotted woodpecker	Insectivore	Least concern	Non-Farmland	Non-crop	2	0.13
Emberiza calandra	Corn bunting	Granivore	Endangered	Farmland	**Crop**	4	0.26
Emberiza citrinella	Yellowhammer	Insectivore	Least concern	Farmland	**Non-crop**	125	8.22
Emberiza schoeniclus	Common reed bunting	Granivore	Least concern	Non-Farmland	Non-crop	1	0.07
Erithacus rubecula	European robin	Insectivore	Least concern	Non-Farmland	Non-crop	7	0.46
Falco tinnunculus	Common kestrel	Carnivore	Least concern	Farmland	**Non-crop**	16	1.05
Fringilla coelebs	Common chaffinch	Insectivore	Least concern	Non-Farmland	Non-crop	34	2.24
Garrulus glandarius	Eurasian jay	Omnivore	Least concern	Non-Farmland	Non-crop	5	0.33
Hirundo rustica	Barn swallow	Insectivore	Vulnerable	Farmland	**Non-crop**	27	1.78

Species	Common name	Feeding guild[1]	Conservation status[2]	Habitat preference[3]	Nesting behaviour[4]	Total abundance	Relative abundance
Jynx torquilla	Eurasian wryneck	Insectivore	Endangered	Non-Farmland	Non-crop	1	0.07
Lanius collurio	Red-backed shrike	Insectivore	Vulnerable	Farmland	**Non-crop**	8	0.53
Luscinia megarhynchos	Common nightingale	Insectivore	Least concern	Non-Farmland	Non-crop	9	0.59
Luscinia svecica	Bluethroat	Insectivore	Least concern	Non-Farmland	Non-crop	1	0.07
Milvus milvus	Red kite	Carnivore	Vulnerable	Non-Farmland	Non-crop	3	0.20
Motacilla alba	White wagtail	Insectivore	Least concern	Farmland	**Non-crop**	44	2.89
Motacilla flava	Yellow wagtail	Insectivore	Least concern	Farmland	**Crop**	81	5.33
Oriolus oriolus	Eurasian golden oriole	Insectivore	Vulnerable	Non-Farmland	Non-crop	10	0.66
Parus ater	Coal tit	Omnivore	Least concern	Non-Farmland	Non-crop	3	0.20
Parus caeruleus	Eurasian Blue Tit	Insectivore	Least concern	Non-Farmland	Non-crop	74	4.87
Parus major	Great tit	Insectivore	Least concern	Non-Farmland	Non-crop	105	6.91
Parus palustris	Marsh tit	Insectivore	Least concern	Non-Farmland	Non-crop	6	0.39
Passer domesticus	House sparrow	Granivore	Vulnerable	Farmland	**Non-crop**	1	0.07
Passer montanus	Eurasian tree sparrow	Insectivore	Vulnerable	Farmland	**Non-crop**	9	0.59
Perdix perdix	Grey partridge	Granivore	Endangered	Farmland	**Crop**	1	0.07
Phasianus colchicus	Common pheasant	Omnivore	Least concern	Farmland	**Crop**	9	0.59
Phoenicurus ochruros	Black redstart	Insectivore	Least concern	Non-Farmland	Non-crop	8	0.53
Phoenicurus phoenicurus	Common redstart	Insectivore	Endangered	Non-Farmland	Non-crop	9	0.59
Phylloscopus collybita	Common chiffchaff	Insectivore	Least concern	Non-Farmland	Non-crop	24	1.58
Phylloscopus trochilus	Willow warbler	Insectivore	Least concern	Non-Farmland	Non-crop	8	0.53
Pica pica	Common magpie	Omnivore	Least concern	Non-Farmland	Non-crop	26	1.71
Picus viridis	European green woodpecker	Insectivore	Least concern	Non-Farmland	Non-crop	9	0.59
Prunella modularis	Dunnock	Insectivore	Least concern	Non-Farmland	Non-crop	1	0.07
Serinus serinus	European serin	Granivore	Least concern	Farmland	**Non-crop**	4	0.26
Sitta europaea	Eurasian nuthatch	Insectivore	Least concern	Non-Farmland	Non-crop	6	0.39
Streptopelia decaocto	Eurasian collared dove	Granivore	Least concern	Non-Farmland	Non-crop	6	0.39
Sturnus vulgaris	Common starling	Insectivore	Least concern	Farmland	**Non-crop**	96	6.32
Sylvia atricapilla	Blackcap	Insectivore	Least concern	Non-Farmland	Non-crop	20	1.32
Sylvia borin	Garden warbler	Insectivore	Least concern	Non-Farmland	Non-crop	6	0.39
Sylvia communis	Common whitethroat	Insectivore	Vulnerable	Farmland	**Non-crop**	25	1.64
Turdus merula	Common blackbird	Insectivore	Least concern	Non-Farmland	Non-crop	89	5.86
Turdus philomelos	Song thrush	Insectivore	Least concern	Non-Farmland	Non-crop	14	0.92
Turdus pilaris	Fieldfare	Omnivore	Least concern	Non-Farmland	Non-crop	5	0.33
Total						*1520*	*100*

[1] Feeding guild classification based on (Chiron *et al.* 2014) and (Henderson *et al.* 2009)

[2] Classification according to the Bavarian Red List for birds (Bayerisches Landesamt für Umwelt 2016): least concern, vulnerable, endangered (including very rare, near endangered, highly endangered and regionally extinct species).

[3] Classification based on EBBC (EBBC 2015) with farmland birds defined as species of which >50% of the population use agricultural land for breeding or feeding

[4] Classification of farmland bird species based on (Hiron *et al.* 2015; Josefsson *et al.* 2017). A subset only including farmland birds (in bold) was used to test for differences in bird richness related to nesting habits of birds primarily utilizing cropland (farmland birds).

Table IV.S3 Effects of landscape heterogeneity on functional groups. Effects of perennial habitat diversity (LandHet, the proxy for non-crop landscape extensification) on species richness of functional groups 'Feeding guild', 'Conservation status' 'Habitat preference' and 'Nesting behaviour'. Only functional groups and spatial scales of models with significant or marginal interactions between LandHet and functional groups are shown. Slopes were tested against zero using contrast matrices and *p*-values of multiple comparisons were adjusted for the False Discovery Rate (Benjamini & Yekutieli, 2001). Significant *p*-values are indicated in bold and marked with asterisks: (*) $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Model	Estimate	SE	z-value	*p*-value	
Feeding guild					
250m					
LandHet Carnivore vs Zero	-0.34	0.32	-1.07	0.348	
LandHet Granivore vs Zero	0.18	0.35	0.53	0.593	
LandHet Insectivore vs Zero	2.54	0.97	2.63	**0.029**	*
LandHet Omnivore vs Zero	0.55	0.36	1.54	0.177	
500m					
LandHet Carnivore vs Zero	-0.63	0.33	-1.91	0.094	
LandHet Granivore vs Zero	0.02	0.4	0.05	0.957	
LandHet Insectivore vs Zero	3.4	0.85	4.01	**<0.001**	***
LandHet Omnivore vs Zero	0.29	0.41	0.7	0.601	
1000m					
LandHet Carnivore vs Zero	-0.44	0.34	-1.29	0.328	
LandHet Granivore vs Zero	-0.12	0.35	-0.34	0.737	
LandHet Insectivore vs Zero	3.47	0.69	5.05	**<0.001**	***
LandHet Omnivore vs Zero	0.3	0.39	0.78	0.485	
2000m					
LandHet Carnivore vs Zero	-0.57	0.39	-1.44	0.214	
LandHet Granivore vs Zero	0.06	0.43	0.14	0.889	
LandHet Insectivore vs Zero	4.36	0.81	5.39	**<0.001**	***
LandHet Omnivore vs Zero	0.33	0.47	0.7	0.602	
3000m					
LandHet Carnivore vs Zero	-0.56	0.47	-1.2	0.328	
LandHet Granivore vs Zero	0.33	0.5	0.66	0.634	
LandHet Insectivore vs Zero	4.67	1.13	4.12	**<0.001**	***
LandHet Omnivore vs Zero	0.31	0.57	0.55	0.648	
Conservation status					
250m					
LandHet Endangered vs zero	-0.26	0.7	-0.38	0.706	
LandHetl Least concern vs zero	2.4	0.7	3.42	**0.004**	**
LandHet Vulnerable vs zero	1.13	0.76	1.49	0.206	
500m					
LandHet Endangered vs zero	-0.06	0.73	-0.09	0.932	
LandHet Least concern vs zero	2.29	0.73	3.13	**0.011**	*
LandHet Vulnerable vs zero	0.94	0.84	1.12	0.392	
1000m					
LandHet Endangered vs zero	0.05	0.66	0.07	0.945	
LandHetl Least concern vs zero	2.16	0.66	3.26	**0.007**	**

Model	Estimate	SE	z-value	*p*-value	
LandHet Vulnerable vs zero	0.81	0.74	1.1	0.408	
Habitat preference					
500m					
LandHet Farmland vs zero	-0.02	1.07	-0.02	0.987	
LandHet Non-farmland vs zero	3.43	1.07	3.2	**0.004**	**
1000m					
LandHet Farmland vs zero	0.02	0.97	0.02	0.983	
LandHet Non-farmland vs zero	3.17	0.97	3.27	**0.003**	**
2000m					
LandHet Farmland vs zero	0.45	1.2	0.38	0.706	
LandHet Non-farmland vs zero	3.92	1.2	3.28	**0.003**	**
Nesting behaviour					
250m					
LandHet Crop vs zero	-0.78	0.32	-2.4	**0.033**	*
LandHet Non-crop vs zero	1.02	0.95	1.08	0.282	
500m					
LandHet Crop vs zero	-0.9	0.32	-2.81	**0.01**	*
LandHet Non-crop vs zero	0.87	1	0.87	0.384	

Chapter V

Growing TREEs for a sustainable future – a guide to the implementation of ecological farming

"To him who devotes his life to science, nothing can give more happiness than increasing the number of discoveries, but his cup of joy is full when the results of his studies immediately find practical applications."

Louis Pasteur cited in René Dubos "Louis Pasteur – Free Lance of Science", Little, Brown and Company, Boston, 1950.

V.1 The burden of agricultural intensification

The green revolution, technological advances and intensive fertiliser and pesticide use in agriculture have pushed productivity to an all-time high. This has allowed for a gradual shift in the producer to consumer ratio in industrialized countries, enhancing human well-being and global food security. However, farm specialization, the removal of natural habitat and other intensive farming practices also cause unprecedented biodiversity declines (Foley *et al.*, 2011), environmental and societal damage. Biodiversity losses are particularly heavy for insects and farmland birds (Hallmann *et al.*, 2017; BirdLife International, 2018). Hence, intensive farming also threatens nature-based ecosystem services, such as soil fertility, biological pest control and pollination. The economic costs of excess nitrogen in the environment, including ground water pollution, climate change and biodiversity loss have been estimated to be twice as high as the contribution of nitrogen fertilizers to European farmer´s income (Sutton *et al.*, 2011). High social costs of intensive agriculture, e.g. the rapid transition of rural societies in Europe, also need to be considered. Similarly problematic is the large-scale damage of agricultural sectors in Africa by the subsidised export of crop overproduction from the EU. Lastly, recent trends indicate a saturation or even decline of yields despite ongoing intensification (Ray *et al.*, 2012).

As ecological, economic and social costs of intensive farming accumulate, new pathways for a more sustainable agriculture (‘ecological farming’) are at the forefront of numerous research efforts. For instance, the EU-funded project Liberation (“LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificATION“) aimed to provide an evidence base for ‘ecological intensification’, whereby yields in conventional farming systems are matched or increased, and negative impacts on the environment minimized by managing biodiversity and associated ecosystem services (Bommarco *et al.*, 2013). This is done by introducing on- or off-field practices that strengthen the system’s natural capacity to self-regulate and resist current and future changes. For example improved habitat quality can promote crop pollinators and natural enemies of pests, thereby reducing the need to spray insecticides or apply fertilizers (Boetzl *et al.*, 2018).

However, despite recent advances in ecological farming, a large amount of scientific knowledge required to tackle the negative externalities of intensive farming is still lacking ('knowledge gap', Figure V.1). More detrimental, though, is the even slower implementation of research findings ('implementation gap', Figure V.1), although the importance of translating research into action has been widely acknowledged, especially in social or health sciences, and conservation biology (Ormerod *et al.*, 2002; Agre & Leshner, 2010; Memmott *et al.*, 2010; Hulme, 2014)

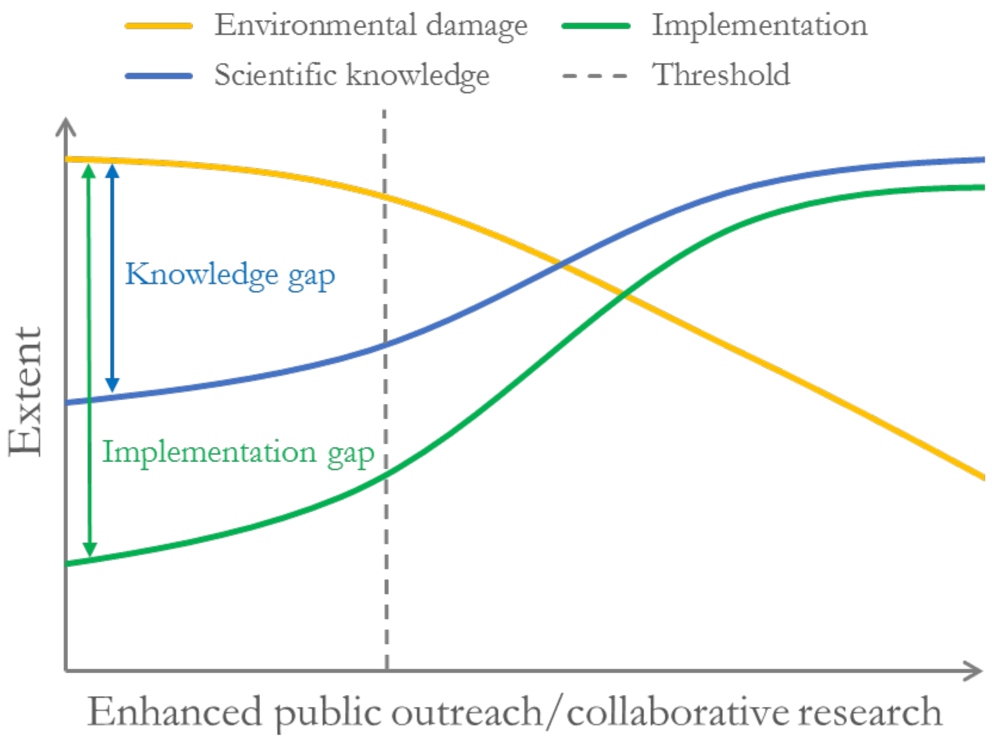


Figure V.1 Closing the knowledge and implementation gap. Scientific knowledge (blue line) needed to alleviate environmental damage (yellow line) accumulates slowly, yet even greater is the divide for research implementation (green line). Enhanced public outreach and collaborative research can reduce these gaps, especially once a certain threshold (grey dashed line) is crossed, beyond which scientific advancement and implementation accelerate due to socio-economic feedback loops (see text).

V.2 Growing TREEs for a sustainable agriculture

What hinders the uptake of research findings related to ecological farming? The list of potential obstacles is long: financial, legal or social constraints, lack of knowledge and professional training prevent stakeholders (farmers, policy makers, extension authorities) from implementing biodiversity-enhancing mitigation methods. However, researchers can overcome some of these obstacles by realising that successful implementation starts on the whiteboard used to sketch out research projects, and extends well beyond the publication of scientific findings (Hulme, 2014). Unfortunately, toolboxes guiding researchers in evading obstacles and creating actionable knowledge (i.e. scientific knowledge that supports stakeholder decision-making) are rare when it comes to the implementation of ecological farming (Geertsema *et al.*, 2016).

Here, we use the analogy of a 'TREE' (Figure V.2) to describe the components required for the successful transfer of research to action, and highlight four crucial steps involved in this process (see Figure V.3 for an illustrated example): **T**ARGET – **R**ESEARCH – **E**NGAGE – **E**XPLOIT/ **E**VALUATE. TREE builds on our discussions with stakeholders during public outreach activities performed in Germany within the project LIBERATION. It challenges scientists to go beyond classical research (Hulme, 2014) by framing their research questions and scientific goals within a wider socio-economic and political context. We also show how the dichotomy between researcher and practitioner perspectives may hinder science implementation. Therefore, TREE is applicable to scientists aiming to develop dissemination strategies or maximize the uptake of scientific knowledge. This perspective is not an exhaustive presentation of the issues around science implementation, but intended to rekindle discussions about ways of doing science.

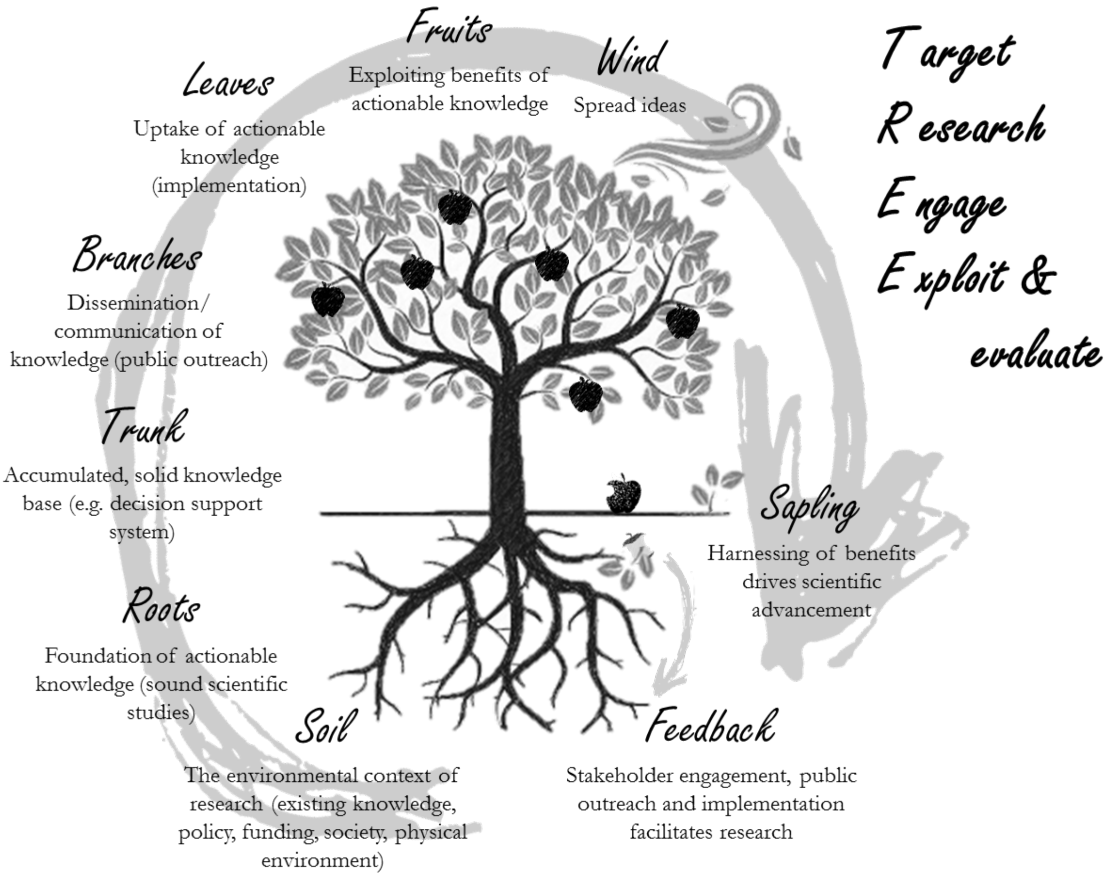


Figure V.2 The TREE concept – Similar to its botanical namesake, TREE requires research to adapt to its environment. It needs a strong (scientific) foundation and a solid (knowledge) base, extensive branching and healthy leaves (successful implementation) to reap it rewards: sustainable farming. Four steps building on these different components are inevitable: i) Target the challenge, ii) Research novel management options and mitigation strategies, iii) Engage with stakeholders and iv) Exploit and evaluate the benefits. Feedback strengthens and accelerates science implementation. Graphic © Sarah Redlich

V.2.1 Step 1: TARGET - Identify relevant challenges and knowledge gaps

Soil is the basis of life. In the context of TREE and ecological farming, the soil entails the physical environment (e.g. study region), but also socioeconomic or political aspects and stakeholder concerns driving or hindering research efforts (Figure V.2, Table V.1). In classical research, where knowledge gaps and agricultural challenges are primarily identified using observations, scientific theory and previous work, ignorance of this wider context might lead to narrow research questions and large amounts of unused knowledge (McNie, 2007). For instance, a farmer's perception of relevance goes well beyond the generalized picture of global importance adherent to most academic research, and focuses on smaller scales (farm or region), personal experiences or observations by peers (Hulme, 2014), and financial, legal or social constraints (Table V.1). Instead of asking "What are the global consequences of pesticide resistance?", an economically driven farmer may ask "Why do I have yield losses due to rape beetle infestations increase, even though I spray expensive insecticides?". Research looking into this matter will be highly relevant to this farmer, especially if potential solutions are affordable, practical and socially acceptable.

Similar considerations apply to most stakeholders: the higher the environmental, economic or health-related costs of intensive farming and the greater the economic and social incentives for solving the problem within the contextual constraints (Table V.1), the greater the relevance of associated research. Therefore, stakeholder consultation at the onset of research projects aids in targeting the most relevant challenges – and increases the likelihood of science implementation ('Target', Figure V.3).

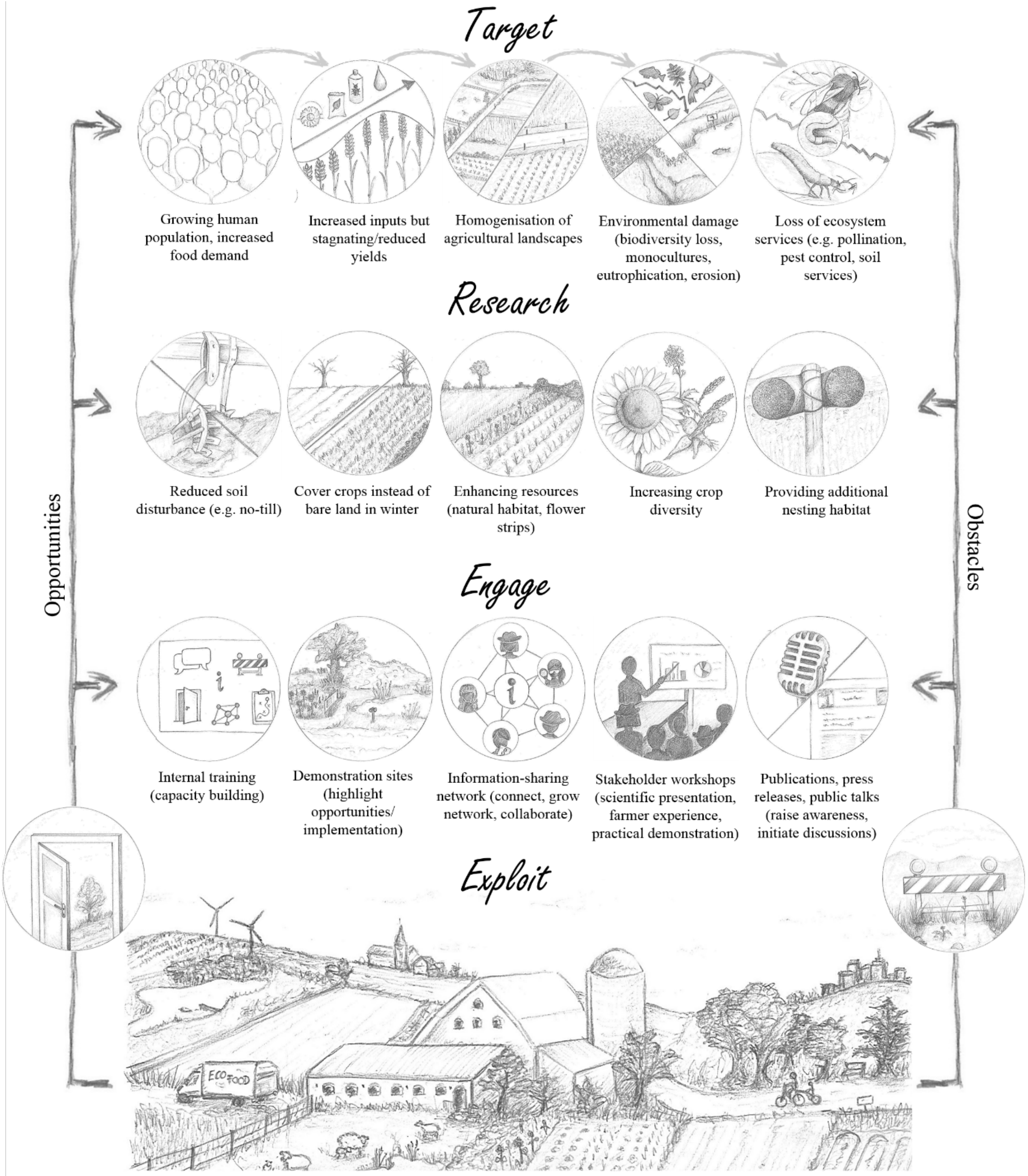


Figure V.3 Illustrated example of TREE based on the EU project Liberation. Target: Interrelated challenges are identified. Research: Mitigation methods are selected and assessed. Engage: Interaction with stakeholders via public outreach. Exploit: Implementation of ecological farming by stakeholders. Throughout the TREE process, obstacles and opportunities feedback into previous steps. Graphic © Sarah Redlich

Table V.1 Varying perspectives: Example of a TREE approach from a researcher's view, with potential obstacles to science uptake based on practitioner's perspective. Different constraints may apply at each of the four steps of TREE. These obstacles can be turned into opportunities by researchers (especially using stakeholder involvement and internal training), or require additional financial, legal or social solutions (highlighted in *italics*). The examples are based on stakeholder discussions within the EU project LIBERATION.

Researcher's perspective		Practitioner's perspective				
TREE approach		FINANCIAL	LEGAL	SOCIAL	KNOWLEDGE	
Step 1 – Target research question  **Aim:** Reduce externalities of agricultural intensification, e.g. increased pest pressure (development of resistance/loss of natural enemies) or costs related to insecticide application. **Question:** How can we enhance biological control of a specific pest to allow for insecticide reductions?	OBSTACLE	Pest organism chosen for study may not cause economic loss everywhere (why spend money on something that is not a problem?) Insecticide is cheap and efficient (no need to replace it), biological control approaches may be costly	Some environmental externalities are driven by regional or national regulations (requirement to annually mow ecological focus areas in the EU Greening scheme lowers biodiversity benefits)	Problem is controversial (biodiversity really beneficial?), experiences public opposition (why change simplified yet tidy-looking fields to fallow, unkept land?) Stakeholders unwilling to participate in consultation	Challenge not perceived as problem (e.g. loss of biological control in agroecosystems "Benefits of biological processes" rarely discussed in agricultural training which focuses on conventional practices	Stakeholder involvement and internal training helps researchers to circumnavigate obstacles
	OPPORTUNITY	Choose major pest (e.g. oilseed rape beetles) economically relevant to most practitioners Highlight off-farm costs of pesticide use (cost-benefit analysis) and *increase costs of pesticides*	*Adapt agricultural policies*	Raise public awareness of challenge Use existing social networks for finding participants, identifying main problems and realistic solutions	Public outreach to increase awareness Give presentation in agricultural schools *Include topics related to benefits of biodiversity in training curriculum*	
Step 2 – Research mitigation method  **Aim:** Develop novel concepts for ecological farming to replace external inputs by ecosystem services **Method:** Assess effectiveness of flower strips for enhancing natural enemies and biological control on fields (ecological intensification)	OBSTACLE	Some interventions (flower strips) need arable land taken out of production, others require costly technology (mixed cropping) Allowing research to be conducted on farm could result in economic costs (yield losses, pest pressure)	Application of mitigation method hindered by agricultural policy (cross-compliance regulations, size restrictions to flower strips, time-consuming mapping required, fear of sanctions)	Practitioners do not want to be involved in research for personal or social reasons (peer pressure)	Research conducted in greenhouses or on small scales may produce unexpected results if methods applied on real farms Confounding factors could mask real effects (e.g. correlations between flower strips and regional pesticide use intensity)	
	OPPORTUNITY	Identify policies that support biodiversity-enhancing measures Guarantee financial compensation for farmers Choose mitigation methods taking into account regional technical constraints	Find alternative mitigation methods (e.g. conservation of existing hedges) or practices that fit within current agricultural policy (e.g. within EU Greening regulation) *Adapt agricultural policy, cross-compliance regulations, regional agri-environmental schemes*	Raise public awareness of importance of research Use existing social networks to identify motivated, open-minded farmers	Try to use real-life farms for experiments Disentangle potentially correlated or interactive effects Use measurements of effect relevant to practitioners (e.g. yield quantity and quality)	

Researcher's perspective		Practitioner's perspective				
TREE approach		FINANCIAL	LEGAL	SOCIAL	KNOWLEDGE	
Step 3 – Engage with stakeholders  **Aim:** Disseminate knowledge of ecological farming and potential management options for enhanced biological control **Method:** Public outreach activities including stakeholder workshops, demonstration sites, public talks	OBSTACLE	Expenses of participating in outreach activities (e.g. travel) Research funding rarely accounts for costs of participants of outreach activities	Some stakeholders may not be allowed to participate in outreach activities	Peer pressure or personal reasons (geographical distance, workload on farm) prevent participation No interest in topic or participation in outreach activity	Unaware of public outreach events (may not have internet or email) No access to scientific journals or barriers related to scientific content or language (English, jargon)	Stakeholder involvement and internal training helps researchers to circumnavigate obstacles
	OPPORTUNITY	Use existing infrastructure that allows stakeholder engagement (annual meetings of agricultural society or field exhibitions) Acquire specific funding for stakeholder participation	Broaden audience (mass media passively reaches more people than workshops)	Use existing social networks to advertise public outreach events Advertise ecological farming as "happy medium" between organic and conventional farming Appropriate timing increases educational value (e.g. flower strips in full bloom) and participation (outside harvest season)	Use existing social networks to advertise public outreach events Identify motivated knowledge brokers or suitable farms for demonstration sites and workshops Internal training (avoid scientific jargon, find appropriate audience, frame take-home message, communicate risks or uncertainties)	
Step 4 – Exploit/evaluate benefits  **Aim:** Increase implementation of interventions related to ecological farming **Method:** Provide sound, scientific data (e.g. effects of enhanced biological control on yield), write policy briefs, provide technical advice. Increase uptake by developing a collaborative project with practitioners, thereby creating landmark farms	OBSTACLE	Excessive costs of establishing intervention (e.g. flower strips) Ecological farming not rewarded financially Costs unequally spread across beneficiaries: farmers pay - neighbours/society benefit	Application of mitigation method hindered by agricultural policy (cross-compliance regulations, size restrictions to flower strips, time-consuming mapping required, fear of sanctions)	Low reputation of practices, e.g. unmanaged arable land (flower strips/set-asides) deemed unhygienic and source of pests/weeds Consumer pressure for low-cost products instead of willingness to pay for healthier food (e.g. biodiversity-certified products)	Lacking support and training of end users (e.g. advice by conservation specialists, extension staff and fellow farmers related to implementation) Insufficient (limited number of studies) or vague scientific evidence Methods may produce unexpected results on real-life farms	
	OPPORTUNITY	Highlight cost savings (reduced insecticide/ environmental costs) Use agricultural policies, guarantee financial compensation for farmers *Establish reliable certification systems ("Biodiversity-friendly product") or payments for ecosystem services*	Find alternative mitigation methods (e.g. conservation of existing hedges) or practices that fit within current agricultural policy (e.g. within EU Greening regulation) *Adapt agricultural policy, cross-compliance regulations, implement regional agri-environmental schemes*	Raise awareness and make sure purpose of research is advertised (put up information signs) Use existing social networks to make stakeholders aware of implementation options and consumers of benefits of ecological farming (and associated costs)	Try to use real-life farms for experiments, disentangle potentially correlated or interactive effects (effects on yield, economic or environment), conduct cost-benefit analysis Create "landmark farms" that allow practitioners to see benefits and how measures were implemented	

V.2.2 Step 2: RESEARCH – identify and assess potential mitigation methods

Research is the "basis of scientific knowledge" (Dicks *et al.*, 2014) - the roots forming the foundation of scientific advancement and implementation. As a general rule: the denser the root network, the stronger the tree. Yet its strength also depends on the identification and evaluation of promising, feasible mitigation methods to targeted agricultural challenges, and the quality of scientific research.

Mitigation methods in ecological farming should be grounded on ecological theory and previous studies, and use self-regulating, natural processes ('Research', Figure V.3). For instance, habitat and crop diversification provides additional resources to beneficial organisms thereby fostering diverse pollinator and antagonist communities (Boetzl *et al.*, 2018; Redlich *et al.*, 2018). However, in addition to having ecological benefits, practices need to fulfil a range of criteria off the scientific radar, including social, technical and legal aspects (Table V.1) (Dicks *et al.*, 2014). These vary among farming systems, municipalities and countries. For instance, in multi-owner farming landscapes such as Germany the pressure to oblige social standards is considerably higher than in landscapes where one's farmland is grouped around a central farmstead. To increase acceptance of proposed mitigation methods by various stakeholders, researchers ought to be aware of potential constraints, and adapt practices accordingly (Table V.1).

Subsequently, the effectiveness of beneficial practices is validated by hypothesis-testing, which assesses influences on biodiversity, ecosystem services and productivity. Research should fulfil the classical requirements regarding replication (account for variability) and independence of data (test for spatial or temporal dependence and correlations with other factors). Additionally, the quantitative assessment using measurement units meaningful to practitioners is integral to producing actionable knowledge. Far from being interested in statistical significance levels, farmers in particular require reliable effect sizes indicating the benefits gained from implementing specific measures (Table V.1).

Consultation with stakeholders and their active involvement in the research process (collaborative research) provides the greatest opportunities for selecting relevant practices, strengthening the experimental design, the reliability of data, and subsequent uptake rates (Hulme, 2014). During the field selection process, researchers should use existing networks established in extension offices or farmer's associations to contact suitable farmers that help to select fields and minimize environmental variation (Memmott *et al.*, 2010).

The accumulated knowledge (the tree trunk) of solid, reliable studies provides the core of future public outreach activities. Ideally, this core takes the shape of a decision support system providing alternative implementation options depending on the farming system or context (Dicks *et al.*, 2014).

V.2.3 Step 3: ENGAGE - Effectively disseminate and communicate research output

It is then time to step outside the relatively narrow confines of the academic environment and branch out into the world (Figure V.2). Public outreach (i.e. science dissemination and communication) provides the means to do so by stimulating critical thinking and promoting the transition from theory to practice.

Dissemination is a targeted activity of promotion and awareness-raising, in which research results are uni-directionally disclosed to stakeholders (research peers, industry, policymakers). For communication, the target group is generally wider (mass media, end users, general public), and the advantage of beneficial practices for society and the environment is communicated through an iterative and multidirectional process (Agre & Leshner, 2010). In classical research, however, public outreach primarily involves scientific presentations and articles in scientific journals, methods limited to a specialized scientific audience. Practitioners rarely have access to the accumulated knowledge base (McNie, 2007), or struggle with a range of barriers related to language and content (Table V.1). Other means of knowledge dissemination (e.g. press releases, policy briefs) are seldom used, either due to time-constraints, lack of funding, incentives or expertise (Wilson *et al.*, 2010).

Effective public outreach requires thorough planning early on, as it is necessary to collate information on the available knowledge base, and identify studies linked to one's own that confirm and support the findings, or offer alternative options (i.e. create a decision support system). Internal training workshops for capacity building among scientists can aid in the planning and execution of outreach activities (define take-home messages, use of adequate terminology; Table V.1).

Active engagement should then involve classical dissemination activities and a range of broader, interactive communication events ('Engage' Figure V3). During outreach activities, motivated practitioners, farmer organizations and biodiversity conservation specialists should act as knowledge brokers (Lomas, 2007), intermediaries bridging the gap between knowledge producers (researchers) and end users (farmers, policy makers). Knowledge brokers translate research findings into appropriate language, set it in the right context (environmental, agricultural, social challenges), add practical experience, guidance on implementation, policy and management advantages or obstacles (Table V.1). Accordingly, they facilitate knowledge transfer, the establishment of an information sharing network (Figure V.3), capacity building and research use.

Visualisation of research is an important component of knowledge transfer, and therefore essential to highlight how nature-based solutions can be implemented and used to make a good living for farmers, and a good life for everyone. Simultaneously, stakeholders need to be aware of uncertainties and emerging risks. It is a scientific obligation to communicate them whenever possible, to enhance the credibility of research and the success rate of implementation. This may involve a clear definition of the environment and conditions under which experiments took place (greenhouse vs. field experiments), how potential confounding factors were controlled, or if results are only expected under specific circumstances (context-dependence) (Hulme, 2014). Decision support systems offer practitioners a tool to select appropriate interventions depending on their own settings (Dicks *et al.*, 2014).

Researchers should follow up all activities with a detailed description of lessons learnt, challenges, opportunities and potential collaborators (e.g. for collaborative research) (Memmott *et al.*, 2010). Recording successes and failures (feedback) is an important step towards increasing the effectiveness of future research, stakeholder engagement and implementation (Figure V.1). Ideally, participating stakeholders spread actionable knowledge by word-of-mouth, and practitioners inspire fellow farmers within their social and economic network by implementing beneficial practices on their own farm ('landmark farms'), consequently creating new branches for knowledge transfer.

V.2.4 Step 4: EXPLOIT & EVALUATE – Implementation of actionable knowledge

Framing targeted research questions related to agricultural challenges, finding possible solutions and rigorously assessing their effectiveness lays the groundwork for successful knowledge transfer – the roots and trunk, so to speak. Effective public outreach using knowledge brokers helps to spread the idea, comparable to the branching of a tree spreading water and nutrients (i.e. knowledge) in different directions. Yet implementing knowledge and exploiting the benefits of ecological farming is the decisive step required to achieve change.

Implementation of ecological farming can be driven by i) policy adaptation to meet environmental goals (e.g. cross-compliance regulations, greening measures or agri-environmental schemes as part of the European Common Agricultural Policy, establishing new certification schemes to reward environmentally-sound farming), ii) society (social and consumer pressure calling for biodiversity-friendly alternatives to food production, inspiration by landmark farms or neighbours), iii) economic incentives (related to agricultural policy or higher market value of biodiversity), or iv) a farmer's personal belief in the advantages of ecological farming. Personal believes are of central importance, as high implementation rates can only be sustained if farmers are convinced of benefits regardless of financial incentives offered, making ecological farming self-sustaining. The scale of implementation can range from small (individual fields or farms) to larger scales (entire communities committing to and working towards a common goal).

There is no one-fits-all solution for the successful uptake of ecological farming. Each practitioner or community needs to define specific goals and identify feasible mitigation methods for her farm/the region, keeping potential socioeconomic, practical and political restrictions and resultant opportunities in mind (Table V.1). Researchers and knowledge brokers can aid in this process by contributing sound, scientific findings, translating and disseminating knowledge, providing policy information and practical advice, as well as thoroughly evaluating the effectiveness of implemented measures. Scientific evaluation strengthens practitioners' trust in ecological farming, and should be used for further communication of findings both within the scientific and public domain.

V.3 Feedback loops facilitate transfer from research to action

Although the demand for ecologically produced food grows steadily, the amount of land under ecological farming is comparably low, with organic agriculture reaching a share of 6.7% and 1.2% in the European Union and worldwide, respectively (Willer & Lernoud, 2018). Our experience indicates that careful selection and assessment of research projects, public outreach, the use of knowledge brokers and collaborative research act as catalysts, i) closing the scientific knowledge gap, ii) accelerating the rate of research implementation and iii) mitigating some of the negative effects of conventional agricultural intensification (Figures V1 & V.3).

Stakeholder involvement plays a crucial role in this process. The more intense the stakeholder interactions (i.e. the greater the input and right of co-determination of stakeholders), the higher the likelihood of successful implementation. Ideally, the accumulated knowledge base and increased exploitation of benefits (i.e. enhanced biodiversity, ecosystem services and yield) will result in a threshold being crossed, beyond which scientific advancement and uptake rates accelerate further due to positive socio-economic feedback loops (Ormerod *et al.*, 2002; Memmott *et al.*, 2010; Geertsema *et al.*, 2016), which facilitates the mitigation of environmental externalities (Figure V.1). As stakeholder engagement is often limited by financial, legal or societal constraints (Table V.1), special funding could increase the likelihood of active participating across all stages of TREE.

V.4 A young TREE that needs to grow

Highly collaborative approaches with stakeholder involvement generate a rewarding two-way exchange, but may also reveal disagreements among researchers and practitioners. Accordingly, all participants require considerable competence in problem-solving and willingness to compromise. Furthermore, researchers may experience low interest amongst the agricultural (and local government) community in ecological farming approaches which can be only overcome by long-term education, professional training of farmers and a new societal and policy framework. Farmers may also be reluctant to implement new methods (risk avoidance), especially if scientific evidence for their benefit is scarce. In the best case, some practitioners may adopt the methods regardless of economic incentives, e.g. because it fits current farm management, farmers are innovators or have personal interests in conserving wildlife e.g. for hunting, bird watching, and others will follow. Yet despite a long list of constraints jeopardizing the success of TREE (Table V.1), identifying potential pitfalls is the first step towards turning obstacles into opportunities (Table V.1). For instance, specific financial support by funding agencies facilitates stakeholder engagement, knowledge brokers break down social barriers and introduction of ecological farming methods in agricultural schools raises awareness.

In the end, benefits of ecological farming (reduced environmental externalities, food security, biodiversity conservation) are reaped and costs shouldered by society as a whole. Consequently, ecological farming methods such as ecological intensification oblige a range of stakeholders (farmers, farmers' organizations, regional authorities, policy makers, scientists, non-governmental organisations, industry and the general public) to contribute towards the TREE process. All the more urgent is the need for researchers to transfer knowledge to people outside the scientific realm and not necessarily familiar or receptive to ecological ideas and concepts, i.e. to "preach beyond the converted", for instance by using social media outlets (Pyke, 2017). It may even pay off to swap scientific reasoning for emotional appeals and 'framing' […] arguments in [catchy and often repeated] 'metaphors' that people already understand and relate to" (Begon, 2017). This is something many scientists will feel hesitant about. And, depending on their research topics and scientific goals, going this extra mile will not necessarily be required. For others that recognize the wider socioeconomic value of their work, TREE may offer some tools as to maximising the impact of research. TREE does not require all-encompassing knowledge of every contextual constraint that may hinder implementation (Table V.1), or flawless execution of each described step. We believe that even inexperienced scientists and those without sufficient funding for intensive stakeholder involvement or public outreach can contribute an important puzzle piece towards closing the knowledge and implementation gap related to ecological farming by planning their research with TREE and its opportunities in mind.

Chapter VI

General discussion

Ecosystem services such as biological pest control, pollination and nutrient cycling are indispensable for crop production, yet suffer from neglect and intensive agricultural management. Ecological intensification can alleviate biodiversity loss and enhance ecosystem services while reducing our reliance on agrochemical inputs. Here, I identified pathways, obstacles and opportunities for ecological intensification. Responses to management or landscape-related mitigation methods differed among functional groups and spatial scales. The reduction of agrochemical inputs may not only mitigate environmental externalities, but was shown to facilitate pest reduction and yield quality. The abundance of natural enemies profited from reduced soil disturbance (no-till), small field sizes and extended crop rotations at intermediate, and an increase in landscape-level crop diversity at small scales. The spatial diversity of cropping systems also facilitated biological pest control, with up to 33% higher pest regulation on local scales. These benefits most likely stemmed from enhanced spatial and temporal resource availability and ease of access to pest-infested fields, especially for epigeal crop-dependent species. Species interactions can result in negative or non-significant biodiversity – ecosystem service relationships, but birds did not affect insect-mediated pest control in our study system. Additionally, bird responses varied from those of natural enemies in that avian biodiversity showed no benefits of landscape-level crop diversity at the spatial scales investigated here. In contrast, total and functional groups richness (insectivorous, non-farmland and non-threatened birds) were enhanced by non-crop landscape heterogeneity. These findings highlight the value of combining on-field and landscape approaches to ecological intensification to increase the overall benefit for biodiversity, productivity and the environment. Yet the implementation of interventions requires scientists to actively engage with stakeholders throughout the research process. Social, economic, technical and legal obstacles to implementation need to be identified and overcome, and research goals redirected to gain the greatest benefit for science, farming and society as a whole.

"You can't go back and make a new start, but you can start right now and make a brand new ending."

James R. Sherman

VI.1 Creating a sustainable future

Humankind bears a great responsibility. Our actions and sometimes careless ignorance of the value and importance of natural resources and processes threatens the stability and resilience of nature, and jeopardizes not only our own existence, but the future of most living organisms. While not the sole culprit, modern industrialized agriculture is one major driver of environmental change. Agriculture played an integral role in the evolution of human society away from hunters and gatherers (Smith, 1998), but it has also dramatically reshaped the surface of the earth by exploiting or deteriorating natural treasures that are not, as sometimes assumed, unlimited and indestructible (Foley *et al.*, 2005). Quite the contrary, we now know that some of our biggest resources – indispensable, biodiversity-mediated ecosystem services such as biological pest control, water filtration and nutrient cycling – are collapsing worldwide, in many cases irretrievably. Human ingenuity may have found ways to deal with these collapses. For instance, hand-pollination of apples may partially substitute losses of wild pollinators in China (Partap & Ya, 2012), and attempts to develop autonomous pollinating microrobots (https://wyss.harvard.edu/technology/autonomous-flying-microrobots-robobees) are ongoing. Nevertheless, human technology and manpower is unlikely to successfully and cost-efficiently replace the whole suite of degraded ecosystem services. Simultaneously, growing food demand accompanied by ongoing health and environmental pressures call for more sustainable farming systems able to maintain current levels of productivity.

Consequently, increased research efforts aiming to gain a comprehensive understanding of biodiversity-ecosystem service relationships in real-life ecosystems and their role in sustainable agriculture are inevitable. Associated research projects build upon ecological theories and knowledge of traditional farming systems, and thrive from the cooperation of scientists and practitioners. One such project was Liberation (LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensification). It aimed to provide the evidence base for ecological intensification, an alternative way of conventional farming which actively manages on- and off-farm biodiversity to enhance essential ecosystem services such as nutrient cycling, pollination and biological pest control. Within this context, I conducted my doctoral thesis research and explored pathways to ecological intensification in winter wheat.

In a comprehensive field study assessing direct and indirect drivers of biodiversity and yield (Chapter II), I showed that reduced soil preparation and high crop rotation diversity had the greatest benefit for crop productivity and the enhancement of natural enemies irrespective of external agrochemical inputs. Yet landscape variables also deserve consideration as tool for ecological intensification. For instance, landscapes with small average field sizes at the 1000m scale and high crop diversity, in particular at local scales up to 500m, respectively increased natural enemy abundances (Chapter II) and biological control of the cereal grain aphid *Sitobion avenae* (Chapter III). At the same time I showed that birds did not influence biological control services in our temperate winter wheat systems (Chapter III), and the response of birds differed from that of natural enemies. Crop diversity at the scales considered here (up to 3000 m radii around study fields) did not influence their richness (Chapter IV). In contrast, heterogeneous landscapes with high habitat diversity, small field sizes, and seminatural habitat rather than cropland cover favoured the diversity of birds, especially insect-feeding, non-farmland and non-threatened birds, across multiple spatial scales (Chapter IV). The latter study also highlighted the need to distinguish between functional groups, as some, such as crop-nesting farmland birds, are disadvantaged by heterogeneity often set as goal for conservation efforts. Last, I used feedback collected throughout Liberation outreach activities to identify obstacles to transferring research into action. This knowledge influenced the development of TREE, a guideline highlighting the role of stakeholder involvement throughout the research process (Chapter V). It encourages scientists to step out of their comfort zone and actively engage with the end users of the knowledge they create: farmers, policy makers and the general public.

VI.2 Field-scale management for ecological intensification

The farm has often been identified as relevant management scale for biodiversity conservation. Accordingly, farm management is an integral part of ecological intensification. Even though cultural, economic, legal and social components also play an important (sometimes underestimated) role, practitioners ultimately bear the responsibility for what happens on their farm and therefore the brunt of the decision-making. This inevitably calls for biodiversity-enhancing measures that are implemented on the farm scale and easily integrated into everyday farm management activities.

Although winter wheat is in some cases grown as cover crop to manage soil erosion, its primary cultivation as cash crop requires a substantial input of agrochemicals. Yield losses are greatest for pathogenic fungi and weed competition, so the application of fungicides and herbicides is seen as almost obligatory in conventional farming systems. The economic damage resulting from arthropod pests such as cereal grain aphids and cereal leaf beetles can be equally high, but is extremely variable depending on growing region and farm. Nevertheless, insecticide is applied prophylactically and usually mixed with other plant protection agents to avoid excess soil compaction and labour linked to additional spraying rounds. Unfortunately, agrochemicals have substantial influences on biodiversity, ecosystem services and productivity (Vitousek Peter M. *et al.*, 1997; Birkhofer *et al.*, 2008; Geiger *et al.*, 2010; Garratt *et al.*, 2011; Krauss *et al.*, 2011; Otieno *et al.*, 2011; Jonsson *et al.*, 2012; Goulson, 2013; Hallmann *et al.*, 2014; Douglas *et al.*, 2015), partly by promoting the development of resistances to chemical substances (Gould *et al.*, 2018). While reductions in their use seem unavoidable, they come at a financial cost with yield losses around 30 % if fertilizers are not applied (Chapter II)(Gagic *et al.*, 2017).

The upside is that reductions in mineral fertilizer input indirectly lowers pest pressure by some arthropod pests. Pests such as *Oulema* larvae or the rose-grain aphid *Metopolophium dirhodum* respond positively to changes in plant quality and density associated with increased nutrient availability, thereby causing enhanced pest pressure (Otieno *et al.*, 2011; Garratt *et al.*, 2018b) and potentially even reductions in wheat quality (Chapter II). For wheat, which is commonly used for breadmaking, milling quality is an important aspect of productivity that determines its market value (Botwright *et al.*, 2002). Decreasing farming intensity may therefore lower pest infestations (Hasken & Poehling, 1995) and to some extent buffer against financial losses. As shown here (Chapter II & III) and elsewhere (Hasken & Poehling, 1995; Garratt *et al.*, 2010; Gagic *et al.*, 2017; Garratt *et al.*, 2018b), however, not all pests decrease with lower fertilizer inputs. Densities of the dominant pest species *Sitobion avenae* were equally high in fertilized and non-fertilized plots (Chapter II & III). Nevertheless, fertilizer amendments have the potential to negatively affect tritrophic interactions and biological pest control (Chen *et al.*, 2010). Adjusting fertilization levels may therefore decrease the need for insecticide applications.

In respect to pest control, my studies showed that the long-term regulation of pests by insecticide was inefficient for most species (with the exception of *Oulema* larvae, Chapter II)(Krauss *et al.*, 2011), and yield suffered from high aphid abundances. Opposed to previous studies (Geiger *et al.*, 2010; Krauss *et al.*, 2011; Macfadyen & Zalucki, 2011; Otieno *et al.*, 2011; Jonsson *et al.*, 2012; Douglas *et al.*, 2015) we did not observe or were unable to test for insecticide effects on predators (Chapter II) and biological control (Chapter III, no natural enemy exclusion cages in insecticide plots). The lack of response is in line with findings of the joint Liberation experiment, although direct and indirect effects on highly mobile natural enemies were likely underestimated because of immigration from adjacent non-insecticide plots (Macfadyen & Zalucki, 2011). Although not directly investigated in this thesis (Chapter IV), evidence for effects of insecticides and other pesticides on birds also exists. Plant protection substances are known to travel through the food chain or reduce the invertebrate prey of insectivorous birds (Geiger *et al.*, 2010; Goulson, 2013; Chiron *et al.*, 2014; Hallmann *et al.*, 2014).

The mobility of pesticides and mineral nitrogen fertilizers extends their impact beyond field boundaries and confronts numerous non-target animals and plants with high, often detrimental levels of substances they are not adapted to (Vitousek Peter M. *et al.*, 1997; Goulson, 2013). Therefore, reduction of agrochemical inputs is likely to have beneficial effects on different levels of biodiversity (from terrestrial and freshwater to marine), ecosystem services and environmental conditions (e.g. reduced acidification and eutrophication) (Vitousek Peter M. *et al.*, 1997; Birkhofer *et al.*, 2008; Filippi-Codaccioni *et al.*, 2010; Geiger *et al.*, 2010; Brittain & Potts, 2011; Krauss *et al.*, 2011; Jonsson *et al.*, 2012; Gagic *et al.*, 2017; Garratt *et al.*, 2018b). For instance, reduction of fertilizer inputs allows farmers to harness below- and aboveground ecosystem services related to soil fertility and pest control suppressed under high mineral nitrogen regimes (Gagic *et al.*, 2017). Similarly, insecticide application could be reduced in fertilized fields with low SOC, or unfertilized high SOC fields because of lower pest abundances and high biological control (Gagic *et al.*, 2017). This practice of ecological intensification is likely to increase the economic value of biological control services (Naranjo *et al.*, 2015), with benefits primarily pocketed by farmers (Zhang *et al.*, 2018).

Apart from agrochemical inputs, the importance of soil characteristics and management for biodiversity and ecosystem services repeatedly resurfaced in my studies and related research within the project Liberation. Soil organic carbon (SOC) content and low soil disturbance were major determinants of soil-dwelling natural enemies and yield quality (Chapter II). Opposed to other studies (Garratt *et al.*, 2018b), yield quantity was not affected. SOC provides important services to biodiversity and productivity, including water retention, nutrient storage and alternative prey (Tilman *et al.*, 2002). Yet the rate of SOC accumulation and degradation greatly depends on the crop rotation, the amount of detrital subsidies, levels of soil disturbance and the fertilization regime (Haddaway *et al.*, 2015). Although organic farming with large amounts of organic fertilizer amendments is usually considered beneficial for SOC, soil quality and productivity (Birkhofer *et al.*, 2008; Yang *et al.*, 2011), intensive soil management for weed control may accelerate SOC depletion on organic (and conventional) farms (Tilman *et al.*, 2002; Williams & Hedlund, 2014). In addition, the mechanical disturbance of the soil causes direct morality of soil-dwelling natural enemies such as predatory carabids and ground-hunting spiders, reduces their abundance and potential to control pests (Tamburini *et al.*, 2015). These predators are particularly important at early stages of pest infestations. They forage on dislodged aphids that have fallen on the ground, thus preventing resettlement (Kromp, 1999). Accordingly, conservation tillage can not only enhance soil fertility, water regulation and weed control, but also pest control

(Tamburini *et al.*, 2016). While insectivorous birds also benefit from conservation tillage, other functional groups such as specialist farmland birds may thrive in conventional tillage systems (McLaughlin & Mineau, 1995; Filippi-Codaccioni *et al.*, 2009). Overall, combined soil conservation practices including the addition of detrital subsidies and organic fertilizer (Chapter II), cover crops and reduced soil disturbance (Chapter II) favors aboveground arthropod biodiversity and a range of ecosystem services (Kromp, 1999; Birkhofer *et al.*, 2008; von Berg *et al.*, 2010; Tamburini *et al.*, 2015, 2016). Lastly, high soil quality reduces yield instability driven by stochastic weather events, and lowers the dependence on external inputs (Cong *et al.*, 2014).

Other soil characteristics do not lend themselves easily to manipulation, and can therefore not be considered appropriate management tools for ecological intensification. Yet depending on the system, soil pH and type can influence crop yield. We did not, however, find correlations between soil pH and wheat productivity (Chapter II). As observed for oilseed rape (Bartomeus *et al.*, 2014), positive effects of pH on yield may be cancelled out by high levels of pest infestations. The amount of loam content in the soil, on the other hand, increased grain weight (Chapter II). Properties such as soil type shape the abundance and diversity of soil biota, thereby influencing essential soil-related ecosystem services such as decomposition and nutrient cycling (Birkhofer *et al.*, 2012).

The benefits of field-scale diversification has often been shown (Kromp, 1999; Rusch *et al.*, 2010; Ratnadass *et al.*, 2012; Kennedy *et al.*, 2013; Dassou & Tixier, 2016; Lichtenberg *et al.*, 2017). In particular, flower plantings next to crops such as wheat, potato and oilseed rape fields facilitate natural enemies and biological control (Tschumi *et al.*, 2015; Boetzl *et al.*, 2018). They can even translate to economic gains (Letourneau *et al.*, 2011; Pywell *et al.*, 2015; Gurr *et al.*, 2016; Tschumi *et al.*, 2016). In our study region, flower strips are relatively common due to extensive agri-environmental schemes subsidizing their implementation, yet were not assessed here. Neither was mixed cropping, which is rather uncommon because of technical barriers (Chapter V). However, one ecological pathway promoting web-building spiders and yield was uncovered: crop rotation diversity. Web-building spiders are likely to benefit from increased temporal resource diversity and reduced chemical input of diverse cropping systems (McLaughlin & Mineau, 1995), while the enhanced nutritional balance increases crop quality (Chapter II)(McLaughlin & Mineau, 1995; Ratnadass *et al.*, 2012). As with other management factors, benefits of temporal crop diversity did not extend across all functional natural enemy groups. The same applied to landscape-level (spatial) crop diversity (hereafter 'crop diversity').

VI.3 Landscape approaches to sustainable agriculture

Next to soil and crop management factors, the role of landscape variables, in particular crop diversity, for biodiversity and ecosystem services was the main focus of my doctoral research. As landscape variables act upon different scales and functional groups (Gabriel *et al.*, 2010; Miguet *et al.*, 2013; Rusch *et al.*, 2013; Shackelford *et al.*, 2013; Jackson & Fahrig, 2015; Martin *et al.*, 2016), scale- and context-specific responses were evaluated whenever possible.

As shown, the effects of crop diversity on arthropod and bird biodiversity and ecosystem services were variable. The abundance of predatory arthropods (leaf-dwelling predators) and parasitoids only responded to crop diversity at small (up to 500m) and large (2000-3000m) spatial scales, respectively (Chapter II & III). These natural enemy groups differ in their dispersal ability, and have been linked to landscape aspects at a range of scales (e.g. 500m (Chaplin-Kramer *et al.*, 2011; Tamburini *et al.*, 2015), 2000m (Thies *et al.*, 2003; Gardiner *et al.*, 2009)). In contrast, bird diversity did not relate to the diversity of arable crop groups in the landscape (Chapter IV).

While arthropod natural enemies (especially less mobile, crop-dependent species such as epigeal predators, (Shackelford *et al.*, 2013)) may rely on higher resource availability and continuity provided by crop diversity (Chapter III, (Schellhorn *et al.*, 2015)), birds may be less reliant or otherwise able to switch to non-crop resources in less diverse cropping systems (Chapter IV). Accordingly, crop diversity may be more important in landscapes with scarce (yet not absent) natural resources ('intermediate landscape complexity hypothesis' (Tscharntke *et al.*, 2005; Josefsson *et al.*, 2017). However, this hypothesis could not be confirmed as no interactions between crop diversity and perennial habitat diversity (as proxy for landscape heterogeneity, Chapter IV) were found. Our hypothesis that correlations between crop diversity and the frequency and intensity of regional insecticide applications could have cancelled out potentially positive effects of crop diversification on bird diversity (Chapter IV) needs yet to be confirmed. As a final thought, the scale of crop diversity effects on birds may have exceeded the spatial scale used here (up to 3000 m) due to the great mobility and foraging distance of some bird species (Jackson & Fahrig, 2015).

Opposed to other studies (Mooney *et al.*, 2010; Mäntylä *et al.*, 2011; Martin *et al.*, 2013), bird predation did not influence insect-mediated biological control. However, overall biological control (assessed using the natural enemy exclusion experiment) related to crop diversity at a wide range of spatial scales (Chapter III). Biological control increased over time and was enhanced by up to 33% at local scales. Lacking correlations of aerial predators and parasitoids with biological control may suggest that ground-hunting predators were responsible for aphid regulation in this system, a correlation possibly masked by sampling deficits (ground-dwellers not assessed) (Henri *et al.*, 2015). While this is in line with findings of the joint Liberation field experiment (Gagic *et al.*, 2017), species interaction at the community level may also dilute biodiversity-pest control relationships (Letourneau *et al.*, 2009). Alternatively, functional group approaches using natural enemy traits may have better predicted biological pest control (Gagic *et al.*, 2015).

Similar to crop diversity, I found opposing relationships between non-crop landscape heterogeneity and biodiversity of different taxa. In general, natural habitats such as hedgerows are key sources of many beneficial organisms, be it pollinators or natural enemies, by providing valuable foraging habitat and dispersal corridors (Dainese *et al.*, 2016). However, positive impacts of non-crop habitat do not always emerge if i) natural enemies are fully absent, ii) natural habitat favours pests rather than predators, iii) crops provide better essential resources for natural enemies than non-crop habitat, iv) natural habitat is insufficient, or v) agricultural practices counteract benefits of natural habitat (Tscharntke *et al.*, 2016). Concurrent with these hypothesis, neither arthropod predators nor parasitoids increased with seminatural habitat cover on either of six spatial scales in the natural enemy exclusion experiment (Chapter III) or the visual surveys (Chapter II). Four of the above mentioned hypotheses could explain these findings. Cereal leaf *Oulema* beetles, which increased with seminatural habitat, benefitted more than arthropods (Chapter II). Predators relying on crop resources, such as carabids, may display no or negative relationships with non-crop habitat (Chapter II & III), with biological control weakened in landscapes with high amounts of seminatural habitat (Caballero-López *et al.*, 2012; Shackelford *et al.*, 2013). Alternatively, local habitat disturbance (Chapter II) and high pesticide inputs (Jonsson *et al.*, 2012) can mask resource-related landscape complexity effects or drive negative responses to landscape simplification (Gagic *et al.*, 2017). Lastly, natural habitat may distract predators away from crops or act as physical barrier to dispersal, hindering immigration into fields (Holland *et al.*, 2012; Ratnadass *et al.*, 2012). The latter hypothesis is partly confirmed by landscape configuration effects on epigeal spiders, which were found to occur less often in landscapes with high edge density (i.e. a large number of crop – non-crop ecotones). On the other hand, smaller fields increase the ease of access into fields, both for epigeal spiders and aphid pests (Chapter II) (Fahrig *et al.*, 2015).

In contrast to arthropods, bird diversity was mostly greater in landscapes with high perennial habitat diversity, more seminatural habitat than cropland and small fields (Chapter IV), despite difference among functional groups. Insect-feeding, non-farmland and common birds increased with heterogeneity. All other groups were unaffected, with the exception of crop-nesting farmland birds that were reduced in heterogeneous landscapes (Chapter IV). Crop-nesting farmland birds are highly adapted to homogeneous, prairie-like landscapes (Hiron *et al.*, 2015), while at the same time being threatened by intensive on-field management (Guerrero *et al.*, 2012).

Neither overall, insect- nor bird-mediated biological control seemed to benefit from seminatural habitat availability (Chapter III). This finding and observed positive effects of crop diversity corroborates the theory that biological control in our system may be determined by agrobiont species such as predatory carabids that depend on crop rather than non-crop resources. Therefore, crop diversification seems a viable option for ecological intensification of insect-mediated pest control and natural enemy abundance and biodiversity (Chapter III), yet conservation of avian biodiversity requires different approaches. The enhancement of compositional or configurational aspects of non-crop heterogeneity (perennial habitat diversity, seminatural habitat, small average fields) do not only promote the diversity of insect-feeding birds which may fulfil pest control services in other agroecosystems (Chapter IV), but also furthers the abundance of predatory spiders (Chapter II). At the same time, specialist functional groups such as crop-nesting birds call for adapted management approaches directly targeting major threats, for instance reduced mowing regimes (Chapter IV). Although the greatest benefits for biological control were observed at the farm scale, the different scales of effect identified here highlight the need to implement landscape management schemes on a range of spatial scales to optimize the positive influence on overall biodiversity and various ecosystem services (Bartomeus *et al.*, 2014).

VI.4 Interactive effects and the value of compensating growth

Although interactions between soil characteristics, on-field management and landscape variables where investigated for natural enemy and bird diversity and biological control in our study system, none where observed. Nevertheless, it is essential to keep potential context-dependencies in mind, as they may influence the effectiveness and success of environmental-friendly farming methods. For example, reduced tillage was shown to be particularly valuable for increasing biological control by predators or parasitoids if fields were located in simple landscapes (Tamburini *et al.*, 2015), although trade-offs with weed control exist in complex landscapes (Tamburini *et al.*, 2016). Similar to tillage, SOC content may also interact with landscape heterogeneity, so that biological control by predatory carabids on high SOC fields suffered most from landscape simplification (Gagic *et al.*, 2017). This joint Liberation study also emphasized that management for high SOC buffers against crop losses and enhances biological control if agrochemical inputs are reduced (Gagic *et al.*, 2017). Viewed from a different angle, ecological intensification (e.g. reduced tillage, SOC management, fertilizer reduction) may prove unsuccessful if landscape contexts and interacting management regimes are unconsidered.

Last, my studies also highlight the ability of wheat to at least partly compensate for suboptimal conditions (e.g. weed competition, infestation with pathogenic fungi, pest damage)(Freeze & Bacon, 1990). For instance, yield reductions due to weed cover and *S. avenae* infestation had a greater negative effect on plant biomass than on grain yield. This indicates that at the levels reached in our system, controlling these factors by agrochemical means is less critical than expected for final crop productivity. While this offers options for reducing prophylactic insecticide applications, additional enhancement of ecosystem services for ecological intensification (e.g. increased pollination or pest control) may not prove successful if other factors become limiting. For instance, oilseed rape can compensate for suboptimal fertilizer inputs to some extent, but the benefits of pollination can only be reaped under sufficient nutrient levels (Garratt *et al.*, 2018a). However, some oilseed rape varieties show different effects, with pollinator-mediated crop yield highest at low nitrogen levels (Marini *et al.*, 2015). For sunflower, pollination benefits were greatest at intermediate nitrogen levels (*c.* 75 kg ha^{-1}), enhancing yield by 25% compared to pollinator exclusions (Tamburini *et al.*, 2017). Following the idea of the minimum law, all essential resources need to be considered, balancing biotic and abiotic inputs with the overall goal (sustainable agriculture and reduction of externalities) in mind. Yet depending on the resource, opportunities for replacement with ecological processes exist.

VI.5 Crossing boundaries and linking arms

Humankind has reached a crossroads. From here, there are two ways forward, one accelerating the ongoing downward spiral of unsustainability, the other forging a common future for all living beings, balancing economic and conservation goals. The latter road is the hardest. Just as climate change requires drastic, global decisions, such as the development of the Kyoto protocol (https://unfccc.int/process/the-kyoto-protocol), biodiversity loss associated with agricultural intensification necessitates humans to rethink set structures and habits on a global scale. Thus farmers are not the only ones to bear the burden of responsibility, since modern agriculture is dictated by social, economic and political aspects that have to be considered (Chapter IV).

As the evidence for biodiversity loss and failures of ecosystem services accumulate, public values regarding nature and biodiversity change. Scientists and the public demand action. In the best case, political and legal responses follow suit (Pe'er *et al.*, 2014), as showcased by recent reforms to the European Common Agricultural Policy ('Greening', EU Regulation No. 1307/2013). Greening obliges farmers to conserve permanent grasslands, diversify their crop rotations and implement ecological focus areas on 5% of their arable land (European Commission, 2014). Similarly, national agri-environmental schemes offer subsidies for the implementation of environmental-friendly farming practices (Stoate *et al.*, 2001). While this is certainly a step in the right direction, the effectiveness of these measure is controversial (Kleijn & Sutherland, 2003; Kleijn *et al.*, 2006; Ekroos *et al.*, 2014; Pe'er *et al.*, 2014; Batáry *et al.*, 2015; Josefsson *et al.*, 2017). Clearly, the function of greening measures, agri-environmental schemes and cross-compliance regulations has to be defined beforehand, as different spatial arrangements and mitigation methods are required depending on the aim of optimizing biodiversity, ecosystem services and health or productivity. At the same time, ecological processes that help to achieve these goals need to be well understood, especially potential synergies, trade-offs and context-specific outcomes.

This is where scientists have to step up to the plate of providing reliable evidence for ecological intensification using methods easily, effectively and cost-efficiently implemented by farmers. The list of potential obstacles to implementation is long (Chapter V). For instance, interactions among different management and landscape factors can result in unexpected outcomes when aiming to transfer results from small-scale, controlled experiments to real agroecosystems (Tylianakis *et al.*, 2008). Thus anticipated benefits for farmers can be limited and their trust in the practical applicability of research lost (Chapter V). Researchers can overcome this problem by using real-life approaches and agroecosystems, while accounting for interfering correlations – and being honest about possible trade-offs or limitations (Chapter II, III & IV) (Hulme, 2014). Similarly, measurement units of effect ought to be relevant to farmers and policy makers, and communicated in an appropriate way (Chapter V)(Born *et al.*, 2009). Accordingly, measures of crop diversity using the Shannon Wiener index are less useful than its translation into 'effective number of crop types' (Chapter III). Furthermore, some tools for ecological intensification are more or less likely to be adopted (Naranjo *et al.*, 2015). Although flower strips are subsidized by agri-environmental schemes, farmers in Germany are hesitant to implement them. In many cases, valuable cropland has to be taken from production, or farmers fear the additional work load (mapping, maintenance), sanctions (by non-compliance in size etc.) or negative feedback from colleagues (flower strips are often thought to propagate weed dispersal)(Chapter V). In contrast, hedge conservation may provide cost-efficient interventions that hardly disturb everyday farming business (Dainese *et al.*, 2016). Therefore, the likelihood of adopting this measure is increased.

Understanding and recognizing potential pitfalls and opportunities (Table V.1) is essential, and greatly facilitated by engaging stakeholders throughout the research project (Chapter V)(Naranjo *et al.*, 2015). Their input is crucial in all four steps of TREE, from targeting appropriate research questions (which agricultural externality has the greatest relevance to farmers and society?), evaluating mitigation methods (which approaches are practical and most effective?), disseminating research findings (knowledge brokers transfer knowledge to action) to implementing ecological intensification (results more credible, involved farmers likely to adopt approaches and act as role model to neighbouring farms)(Chapter V). Lastly, achieving real change requires researchers to leave their comfort zone, step outside the box and integrate socioeconomic, cultural, practical and legal aspects often ignored in classical research (Stoate *et al.*, 2001). This postulates linking arms with famers, policy makers and scientists with different academic backgrounds.

Yet changing the way in which food is produced and thereby foisting the responsibility off on farmers, politics or science is not enough. Sustainability also relies on changes in consumer behaviour (shift towards a plant-dominated diet and organic products) as well as strategies to reduce food wastage, on household, national and global scales (Foley *et al.*, 2011). For this to happen, stakeholders need to be aware of the ecological value of ecosystem services such as biological control, and how changing consumer/production behaviour benefits not only crop production but also the wider society. Putting an economic value to ecosystem services helps in this process, although numerous benefits associated with extensified production (e.g. insecticide reductions) are difficult to assess (Naranjo *et al.*, 2015). How does one measure the value of human life and health, or the extinction of an animal or plant species? Nevertheless, trying to assess the public understanding of ecosystem services and their value, and the willingness to pay for sustainably grown food is a first step towards increasing public awareness and facilitating change. Additionally, emotional appeals that people understand (Begon, 2017) or calls for ethical considerations such as fairness and altruism encourages behaviour, 'which is profit sacrificing, but which improves economic efficiency by reducing environmental externalities' (Colman, 1994).

VI.6 Conclusion

Recent evidence of extensive biodiversity loss has spurred renewed discussion about the sustainability of modern farming. While humankind greatly relies on intensive crop production to meet the demands of an ever-growing population, the resulting harm for the environment and society as a whole outweighs the apparent benefits. Accordingly, changes in agricultural management are urgently needed, and ecological intensification (i.e. utilizing biodiversity-mediated ecosystem services to balance productivity – conservation goals) presents itself as possible solution. Here, I offer evidence for the effectiveness of ecological intensification on various scales, from adjustments of on-field management practices to the preservation of valuable landscape characteristics. I highlight the need to conserve soil services, temporal and spatial crop diversity and resource heterogeneity. Simultaneously, ecological intensification requires scientists to contemplate scale- and context-specific effects, and their differential influences on functional species groups and ecosystem services. During repeated outreach activities conducted within the EU project Liberation, my attention was also directed towards possible obstacles to ecological intensification, mainly related to the implementation of beneficial interventions. Although farmers are the 'executive organ', their decisions and actions are largely driven by economic, social, technical and legal factors. In turn, whatever happens on a farm feeds back to society as a whole, influencing human well-being, political and socioeconomic structures. Accordingly, solving environmental issues related to agriculture requires interdisciplinary, whole-system approaches to research, with stakeholder participation throughout. Concentrating on relevant research questions, practical interventions and active dissemination of scientific findings will enhance our understanding of mechanisms behind biodiversity loss and how to address them. In this respect, my thesis is a small, yet important puzzle piece towards sustainable agriculture.

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Chapter II has been submitted to Proceedings of the Royal Society B as: Redlich, S.*, Martin, E.A. & Steffan-Dewenter, I. (under review). Ecological pathways to high yield in conventional cereal systems. *Correspondence author (contributed *c.* 80 – 90 % to this study).

Participated in	Author Initials Responsibility decreasing from left to right		
Study design and methodology	SR	ISD	EAM
Data collection	SR		
Data analysis and interpretation	SR	ISD/EAM	
First draft of manuscript	SR		
Editing of manuscript	SR	ISD/EAM	

Acknowledgements

We thank the farmers for kindly permitting us to work on their land, and Matthias Jäger, Verena Seiffert and Florian Haydn for assistance in the field and lab.

Funding

This study was performed within the FP7 project LIBERATION (“LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificatION“), funded by the European Union, grant number: 311781.

Sarah Redlich Prof. Dr. Ingolf Steffan-Dewenter Dr. Emily A. Martin

Chapter III has been accepted as: Redlich, S.*, Martin, E.A. & Steffan-Dewenter, I. (2018) Landscape-level crop diversity benefits biological pest control. Journal of Applied Ecology. *Correspondence author (contributed *c.* 80 – 90 % to this study).

Participated in	Author Initials Responsibility decreasing from left to right		
Study design and methodology	SR	ISD	EAM
Data collection	SR		
Data analysis and interpretation	SR	ISD/EAM	
First draft of manuscript	SR		
Editing of manuscript	SR	ISD/EAM	

Acknowledgements

We thank the editors and three anonymous reviewers for their helpful comments. We thank the farmers for kindly permitting us to work on their land, and Matthias Jäger and Verena Seiffert for assistance in the field.

Funding

This study was performed within the FP7 project LIBERATION ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificatION"), funded by the European Union, grant number: 311781.

Sarah Redlich Prof. Dr. Ingolf Steffan-Dewenter Dr. Emily A. Martin

Chapter IV has been accepted as: **Redlich, S.***, Martin, E.A., Wende, B. & Steffan-Dewenter, I. (2018) Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. PLOS ONE. *Correspondence author (contributed *c.* 70 – 80 % to this study).

Participated in	Author Initials Responsibility decreasing from left to right		
Study design and methodology	SR	EAM	BW
Data collection	SR	BW	
Data analysis and interpretation	SR	EAM	ISD
First draft of manuscript	SR		
Editing of manuscript	SR	ISD/EAM	

Acknowledgements

We are grateful to the editor and two anonymous reviewers for their constructive comments. We thank the Lower Franconian farmers and landowners who permitted us to work on their land and made this study possible.

Funding

This study was performed within the FP7 project LIBERATION ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificatION"), funded by the European Union, grant number: 311781, the German Research Foundation (DFG) and the University of Würzburg (funding programme Open Access Publishing)

Sarah Redlich

Dr. Beate Wende

Prof. Dr. Ingolf Steffan-Dewenter

Dr. Emily A. Martin

Chapter V has been submitted to the Practitioner's Perspective of the Journal of Applied Ecology as: Redlich, S.* & Steffan-Dewenter, I. (under review). Growing TREEs for a sustainable future – a guide to the implementation of ecological farming. *Correspondence author (contributed *c.* 90 % to this study).

Participated in	Author Initials	Responsibility decreasing from left to right
Concept	SR	ISD
Graphical illustration	SR	
First draft of manuscript	SR	
Editing of manuscript	SR	ISD

Acknowledgements

We thank Audrey St-Martin, our knowledge brokers Anne Wischemann (biodiversity conservation specialist) and Werner Kuhn (demonstration site farmer), and all participants of stakeholder workshops for making public outreach activities a full success, and sharing valuable insights regarding challenges and opportunities of implementation. Klaus Erdle and Südzucker for the invitation to present the idea of ecological intensification in the plant protection commission of the German Agricultural Society and during field exhibition days in 2016. All fellow Liberation scientists and collaborators (Xerces, FAO) for information-sharing and support. We thank Emily Poppenborg Martin for valuable comments on the manuscript.

Funding

Funding was provided by the European Union to the FP7 project LIBERATION ("LInking farmland Biodiversity to Ecosystem seRvices for effective ecological intensificatION"), grant number: 311781.

Sarah Redlich Prof. Dr. Ingolf Steffan-Dewenter

Publication list

Publications as part of doctoral thesis

Redlich, S., Martin, E.A. & Steffan-Dewenter, I. (under review) Ecological pathways to high yields in conventional cereal systems. *Proceedings of the Royal Society B*

Redlich, S., Martin, E.A. & Steffan-Dewenter, I. (2018) Landscape-level crop diversity benefits biological pest control. *Journal of Applied Ecology*; 00:1–10. (in press). https://doi.org/10.1111/1365-2664.13126

Redlich, S., Martin, E.A., Wende, B. & Steffan-Dewenter, I. (accepted) Landscape heterogeneity rather than crop diversity mediates bird diversity in agricultural landscapes. *PLOS ONE*

Redlich, S. & Steffan-Dewenter, I. (submitted) Growing TREEs for a sustainable future – a guide to the implementation of ecological farming. *Practitioner's Perspective* of *Journal of Applied Ecology*.

Additional publications

Gagic, V., Kleijn, D., Báldi, A., Boros, G., Jørgensen, H.B., Elek, Z., Garratt, M.P.D., de Groot, G.A., Hedlund, K., Kovács-Hostyánszki, A., Marini, L., Martin, E., Pevere, I., Potts, S.G., **Redlich, S.**, Senapathi, D., Steffan-Dewenter, I., Świtek, S., Smith, H.G., Takács, V., Tryjanowski, P., van der Putten, W.H., van Gils, S. & Bommarco, R. (2017) Combined effects of agrochemicals and ecosystem services on crop yield across Europe. *Ecology Letters*, 20, 1427–1436.

Garratt, M.P.D., Bommarco, R., Kleijn, D., Martin, E., Mortimer, S.R., **Redlich, S.**, Senapathi, D., Steffan-Dewenter, I., Świtek, S., Takács, V., Gils, S. van, Putten, W.H. van der & Potts, S.G. (2018) Enhancing Soil Organic Matter as a Route to the Ecological Intensification of European Arable Systems. *Ecosystems*, 1–12.

Redlich, S., Clemens, J., Bader, M.K.-F., Pendrigh, D., Perret-Gentil, A., Godsoe, W., Teulon, D., Brockerhoff, E.G. (in revision) Identifying new associations between invasive aphids and Pinaceae (pines, spruces, firs) using plant sentinels in botanic gardens. *Biological Invasions*

Acknowledgements

Even though being a PhD student sometimes made me feel like a lone warrior, in truth I would not have come this far if it hadn't been for a variety of people that directly or indirectly supported and guided me on the way.

I would like to thank **Prof. Dr. Ingolf Steffan-Dewenter** for the chance of being part of an interesting project and a wonderful working group, for fruitful discussions and support. Thank you for your trust and numerous chances to prove myself and progress as a researcher. My special gratitude extends to my co-supervisor, **Dr. Emily Poppenborg Martin**, for invaluable advice on experimental design, statistics, ArcGIS and writing manuscripts. I very much appreciated your open door policy. I am also grateful to **Prof. Dr. Ricarda Scheiner**, not only for her support in terms of funding applications, but for taking the time to be part of my thesis committee.

This thesis would not have been possible without the **Liberation project** and the wonderful, diverse **team of scientists** involved in it. The project offered a variety of opportunities for collaborations and scientific exchange, and I very much enjoyed experiencing different cultures (and food) during annual meetings.

I also owe my deepest gratitude to **all farmers** I talked to and worked with in the Liberation project. Thank you for lending an ear to our ideas, providing advice, insights and fields for experiments, for participating in surveys and workshops, and always sparing some time for a friendly chat (although it took some getting used to the Franconian dialect). Special thanks to Südzucker and the manager of Gut Gieshügel for additional technical support.

It was a particular pleasure to organize and conduct various public outreach activities. In this context, my gratitude extends to **Dr. Audrey St-Martin** (for your humour, organizational talent and dedication to science dissemination), **Anne Wischemann** (biodiversity conservation specialist) and **Werner Kuhn** (demonstration site farmer), without whom these activities would not have been possible.

A big thank you to **my department colleagues** for warmly welcoming me into the working group and stimulating interesting discussions of work-related or private nature. I very much enjoyed exchanging ideas about statistical analysis, experimental design, field selection procedures as well as parenting. Special thanks to **Dr. Dieter Mahsberg** (for lunch chats, child-friendly entertainment and visiting Sophia's school) and **Dr. Jens Joschinski** (for crazy R tricks, statistical advice and discussions about babies, nappies and sleep deprivation). A big thank you to my former (**Dr. Beate Wende**, for your help with field/lab work and public outreach) and current office mates (**Dr. Alice Classen**, **Toni**, **Veronika**) for lending an ear, sharing knowledge and laughter, providing distraction, empathy and advice whenever needed.

I am indebted to the **technical, administrative and support staff** of the Department and beyond for their unconditional support related to IT, technical or bureaucratic issues. Whether GIS nightmares (Amy), computer break-downs (Thomas I.), financial matters (Michaela), complicated paperwork (Birgit), fieldwork (Verena), equipment (mechanical workshop), funding applications (Frau Esgen), or last minute travel authorizisations (Herr Henglein), help was always closeby. A special thanks to Matthias Jäger, for invaluable help in the field and with species identification, and to the Geography department for help with soil sampling and analysis.

My PhD thesis would only have been half as much fun and less rewarding without **my Bachelor and Master students** (Nadine, Florian, Bettina, Karin, Maren, Alexandra). You taught me project management and teaching skills… and a whole lot of patience. It was great to see you thrive on a challenge!

Thank you also to Günter Friedmann ("Insektenfreundliche Sonnenblumen"), Erdenwerk Würzburg, LZR, „three able men and a digger", Dr. Nuss soil analysis, Bingenheimer Saatgut, all ÄELFs (Uffenheim, Karlstadt, Würzburg, Schweinfurt, Aschaffenburg, Kitzingen), LfL, Sommerhausen Naturstein, the muncipality of Dettellbach, BayWa, Ingenieursbüro Hetterich, Katz Biotech, Michael Andreas Fritze (Laufkäferbestimmung) and Theo Blick (Spinnenbestimmung). Geographic land use and habitat data was contributed by

Stmelf (Alois Schmidtner), LfL (Melanie Treisch) and the Bayerische Vermessungsamt (Erich Eisenschmid).

Funding for my doctoral research was provided by the European Union (grant number: 311781), the German Research Foundation (DFG) and the University of Würzburg (funding programme Open Access Publishing), and BayFor (initiation of a collaborative research project). Additionally, I am grateful to the mentoring and qualification program, the coordinators Ljubica Lozo and Rose Liebert, and my mentor Nina Farwig for offering training and career advice.

A big thank you to all those people not listed here, but encouraging, helping and motivating me along the way.

Finally, a heartfelt thank you to **my family**. You gave me the freedom to become independent yet have always supported me, sometimes from a far distance, and especially in our darkest hours. Thank you **Stefan** for going on adventures with me, to the end of the world and back again (and it was a very bumpy ride indeed), for your love, encouragement and ability to make me laugh, whatever may come. And the biggest of hugs to our giggly, wriggly, jiggly daughters, **Sophia and Chiara**. Life would be so incredibly boring without you!