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Landscape-scale mechanisms of biological pest control in a South Korean agricultural landscape

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Summary

Biological pest control is a major ecosystem service provided by natural enemies to world crops. However, current understanding of how to manage this service in real-world landscapes is limited by our lack of knowledge of the factors determining landscape-scale pest control, enemy diversity and the relationship between the two. In order to clarify how biological control is provided at large spatial scales, and how it can be improved, this thesis explores the mechanisms determining large-scale pest control provision and natural enemy diversity in a South Korean agricultural landscape.

Landscape complexity is known to benefit natural enemies, yet it is unclear whether and how this translates into increased pest control, damage avoidance and yields. In a field exclusion experiment replicated along a gradient in landscape complexity, characterized by increasing amounts of seminatural habitat around fields, pest control of aphids and Lepidoptera was shown to depend on interactions occurring between functional guilds of natural enemies. Control of Lepidopteran larvae by flying insect enemies increased with the proportion of seminatural habitat around fields. However, so did negative interactions between flying insects and birds. Thus, negative enemy interactions constrained Lepidopteran control in complex landscapes. This effect impacted all levels from pests, to herbivory, to yields. These results suggest that by altering the outcome of trophic interactions between natural enemies, landscape complexity may promote ecosystem services as well as disservices.

In contrast, despite a range of positive and negative interactions between enemies, landscape complexity positively impacted total pest control of aphids. Similarly to Lepidoptera, aphids were best suppressed by the guild of flying insect enemies, whose effects were strongest under conditions of high landscape complexity. Interactions between flying insects and ground-dwellers were complementary in all landscapes, whereas birds had no overall impact on aphid control. Overall, these results suggest that flying insects including syrphids, parasitoid and predatory wasps show the highest potential for improvement of pest control particularly in complex landscapes. However, their effectiveness depends on limiting negative interactions with other enemies, thus on our ability to rigorously manage enemy diversity at all relevant spatial scales.

Effects of landscape complexity on enemy diversity are most frequently investigated according to the amount of (semi)natural habitat around fields, i.e. landscape composition. However, this parameter is often highly correlated with landscape diversity and configuration. In order to disentangle the relative importance of these and local factors for enemy diversity across scales, seven enemy taxa were sampled along uncorrelated gradients in landscape composition, diversity and configuration. Instead of habitat amount, a complex configuration positively influenced most natural enemies at all scales. Interactions between local and landscape factors were found only for birds. Further, high enemy diversity was not reflected by low crop damage. This study shows that enemies respond to distinct landscape factors across scales, thus providing important windows of opportunity to manage potentially contrasting outcomes of enemy diversity and ecosystem service provision in agricultural landscapes.

Theoretical exploration of landscape-scale pest control mechanisms yielded further insights. In a spatially-explicit model, the consequences for pests of intraguild predation (IGP) between enemies were found to depend on landscape complexity. In landscapes with high amounts of seminatural habitat and low spatial autocorrelation (high configurational complexity), IGP by vertebrate predators led to a release of shared herbivorous prey, as predicted by IGP theory. However, in landscapes with low amounts of habitat or high autocorrelation, IGP led to increased predation pressure on herbivorous prey. This result is explained by differences in the local stability of mesopredators across landscapes. In simple landscapes with locally unstable mesopredators, top predators stabilized predator-prey interactions and led to higher predation pressure than with mesopredators alone. These findings confirm empirical results of this thesis showing that landscape complexity may alter the outcome for pests of trophic interactions between natural enemies. Implications for empirical studies of predator-prey interactions include the importance of measuring turnover dynamics of predators and prey at large spatial scales, and show that effective implementation of landscape-wide biological pest control may ultimately depend on the relative population stability across landscapes of pests, arthropod and vertebrate natural enemies.

Zusammenfassung

Biologische Schädlingskontrolle ist eine der wichtigsten Ökosystemdienstleistungen weltweit. Die gezielte Nutzung dieser Leistung ist jedoch durch mangelndes Verständnis jener Faktoren, welche die Schädlingskontrolle auf Landschaftsebene, die Diversität der Feinde, als auch deren Wechselwirkungen bestimmen, nur bedingt möglich. Die vorliegende Doktorarbeit untersucht die großräumigen Mechanismen biologischer Schädlingskontrolle und der Diversität natürlicher Feinde in einer Agrarlandschaft in Süd-Korea. Ziel der Studie war es herauszufinden, wie die Leistung der Schädlingskontrolle auf Landschaftsebene erbracht wird und möglicherweise verbessert werden kann.

Komplexe Agrarlandschaften begünstigen die natürlichen Feinde von Pflanzenschädlingen. Es ist jedoch weitgehend unbekannt, ob und wenn ja wie sich diese Effekte in Form von Schädlingsreduzierung, Schadensvermeidung an Nutzpflanzen und höheren Ernteerträgen äußern. Anhand von Ausschlussexperimenten, repliziert unter variierenden Landschaftsanteilen halbnatürlicher Habitate, wurde nachgewiesen, dass die Schädlingskontrolle von den vorherrschenden Interaktionen zwischen Feinden abhängt. Während eine größere Anzahl von Habitaten einerseits die Kontrolle von Schmetterlingsraupen durch fliegende Insekten erhöhte, führte sie gleichzeitig zu einer Steigerung der negativen Interaktion zwischen fliegenden Insekten und Vögeln. Im Endeffekt wurde die Kontrolle von Schmetterlingen in komplexen Landschaften durch negative Interaktionen zwischen Feinden auf allen Ebenen beschränkt; von der Anzahl an Schädlingen, bis hin zu Fraßschäden und Ernteertrag. Diese Ergebnisse legen nahe, dass Landschaftskomplexität Ökosystemdienstleistungen sowohl positiv als auch negativ beeinflussen kann.

Im Gegensatz dazu hat der Grad an Landschaftskomplexität die Bekämpfung von Blattläusen positiv beeinflusst. Ähnlich wie bei den Schmetterlingen wurden die Blattläuse am effektivsten durch fliegende Insekten bekämpft, deren Einfluss bei hoher Landschaftskomplexität am stärksten war. Interaktionen zwischen fliegenden und Boden-Arthropoden haben sich in allen Landschaften ergänzt, während Vögel keinen Nettoeinfluss hatten. Diese Ergebnisse deuten darauf hin, dass fliegende Insekten (Schwebfliegen, parasitoide und räuberische Wespen) das höchste Potential zur Verbesserung der Schädlingskontrolle in komplexen Landschaften aufweisen. Ihre Effektivität hängt jedoch vom Vorhandensein negativer Interaktionen mit anderen Feinden ab, und damit von unseren Möglichkeiten, die Diversität von Nützlingen auf relevanten räumlichen Skalen gezielt zu beeinflussen.

Die Effekte von Landschaftskomplexität auf die Nützlingsdiversität werden meistens anhand der Anzahl (halb)natürlicher Habitate, sprich Landschaftskomposition, untersucht. Dieser Parameter korreliert jedoch oft mit der Landschaftsdiversität und -konfiguration. Um die relativen Bedeutungen von Landschafts- und lokalen Parametern zu entwirren, wurden sieben Taxa von Feinden entlang unkorrelierter Gradienten dieser Parameter untersucht. Anstatt der Anzahl von Habitaten, hatte eine komplexe Landschaftskonfiguration einen positiven Einfluss auf die meisten Feinde über alle räumlichen Ebenen. Eine Interaktion zwischen lokalen und Landschaftseffekten fand lediglich bei den Vögeln statt. Eine hohe Diversität an Feinden äußerte sich nicht in niedrigen Fraßschäden. Laut dieser Ergebnisse reagieren Feinde auf unterschiedliche Landschaftsfaktoren entlang räumlicher Skalen. Diese Unterschiede könnten wichtigen Handlungsspielraum bieten, um Effekte von Artenvielfalt und Ökosystemdienstleistungen auf Landschaftsebene zu steuern.

Darüber hinaus bot eine Modellierung der Mechanismen der Schädlingskontrolle weitere Einblicke. Anhand eines räumlich-expliziten Modells wurde es nachgewiesen, dass der Einfluss auf die Schädlingsdichte von „intraguild predation“ (IGP) zwischen Feinden von der Landschaftskomplexität abhängt. In komplexen Landschaften, verringerte IGP durch Wirbeltierräuber den Bejagungsdruck auf herbivore Beute, der IGP Theorie entsprechend. In einfachen Landschaften, führte IGP jedoch zu einem erhöhten Jagddruck auf Beute. Dieses Ergebnis lässt sich durch Unterschiede in der Stabilität von Mesoprädatoren zwischen Landschaften erklären. In einfachen Landschaften mit lokal instabilen Mesoprädatoren, stabilisierten Top-Prädatoren die Jäger-Beute Interaktionen und verursachten einen höheren Bejagungsdruck, als nur mit Mesoprädatoren allein. Diese Resultate bestätigen die empirischen Ergebnisse dieser Arbeit in dem Sinne, dass Landschaftskomplexität die Folgen für Schädlinge durch Interaktionen zwischen Feinden verändern kann. Fluktuationsdynamiken von Räuber- und Beutetieren sind folglich auf großen räumlichen Skalen zu erfassen. Außerdem wird deutlich, dass eine effektive Umsetzung von landschaftsumgreifender, biologischer Schädlingskontrolle letztendlich von der relativen Populationstabilität von Schädlingen, Arthropoden- und Vertebratenräubern abhängt.

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All photographies by E. A. Martin.

Chapter 1

1. Synopsis

1.1. Introduction

Why biological pest control?

The biological control of arthropod pests by naturally occurring enemies is an essential ecosystem service provided to world crops. Arthropod pests are estimated to destroy ca. 10% of world crops before harvest (Oerke, 2006). Even when chemical pesticides are used to control pest populations, natural enemies account for up to 90% of pests´ mortality (Pimentel, 2005). The service of biological pest control is all the more necessary due to the harmful nature of pesticides for environmental and human health, and to increased risks of pest outbreaks caused by pests´ rapidly evolving resistance to pesticides (Naylor and Ehrlich, 1997). Agricultural practices aimed at reducing or avoiding the use of chemical pesticides rely on the effectiveness of natural enemies for crop productivity. Decreasing the harmful side-effects of agriculture, while maintaining or increasing crop yields, is one of the paramount challenges of 21st century human society (Bommarco et al., 2013), and enhancing the ability of natural enemies to control pests represents a potentially effective solution to this challenge.

State of the art

To date, several approaches have been proposed to enhance natural enemy populations and pest control function in agricultural fields. Reducing the local intensity of farming practices, for instance by replacing conventional chemical inputs with organic fertilizer and pesticides, or locally homogeneous crops with locally diverse polycultures, have often been found to increase biodiversity in general (Kremen and Miles, 2012) and many natural enemies in particular (Langellotto and Denno, 2004; Bengtsson et al., 2005). In addition, natural enemies have been found to react to the structure of the landscapes surrounding agricultural crop fields. In landscapes with high amounts of non-crop habitat, such as seminatural hedges, old fallows, remnant trees, or forest patches, many organisms including natural enemies are more species-rich and abundant than in simple landscapes formed of homogeneous cropland (Bianchi et al., 2006; Tscharntke et al., 2012). This effect is due to natural or seminatural habitats providing sources of food, overwintering areas, refuges from predation, and other resources for most pest or non-pest organisms inhabiting agricultural areas (Bianchi et al., 2006; Janssen et al., 2007). In agricultural landscapes with high disturbance levels within crop fields themselves, these areas are often the sole permanent habitat type in the landscape, from which species may spill-over into crop fields, where resources are complementary, but unstable (Rand et al., 2006). The composition and spatial configuration of habitats determine the level of overall complexity or heterogeneity of the landscape (Fahrig et al., 2011): landscapes are considered complex when they contain high amounts of non-crop habitats, high habitat diversity, and/or a fine-grained network of habitat patches. Species or functional groups are found to respond to this complexity at different spatial scales, from a few hundred meters to several kilometers (Steffan-Dewenter et al., 2002). These scales appear to vary among organisms according to body size, dispersal abilities and possibly trophic level and degrees of specialization (Chaplin-Kramer et al., 2011; Tscharntke et al., 2012).

Fewer studies have investigated the effects of landscape context and local management intensity on pests and the function of pest control itself. Of these, many show increased rates of predation or parasitism with decreasing management intensity and increasing proportion of non-crop habitats in the landscape (e.g., Thies and Tscharntke, 1999; Bianchi et al., 2005; Roschewitz et al., 2005; Thies et al., 2005). However, effects on the pests themselves remain equivocal, and measures of the ultimate consequences for crops in terms of damage and yields are rare (Chaplin-Kramer et al., 2011). In addition, only few studies have explored the effects of landscape context on actual reduction of pests by natural enemies, compared to situations in which no enemies are present (Gardiner et al., 2009; Thies et al., 2011; Chaplin-Kramer and Kremen, 2012; Holland et al., 2012; Rusch et al., 2013). As many distinct factors are likely to influence the distribution of pest populations across landscapes, experiments are necessary that isolate effects of natural enemies from the underlying spatial variation of pests (Chaplin-Kramer and Kremen, 2012).

Thus measured, the strength of actual pest suppression by natural enemies may not show a direct relationship to enemy diversity in the same landscapes (Letourneau et al., 2009). Interactions between natural enemies can take place that modify the strength of trophic cascades, with variable consequences for pests and crops (Duffy et al., 2007). Such interactions may be additive or synergistic (positive interactions), neutral, or antagonistic (negative interactions), and are linked with mechanisms of niche partitioning or facilitation, functional redundancy, and intraguild predation or behavioural interference, respectively (Straub et al., 2008; Letourneau et al., 2009). If negative interactions take place between different enemy species, increasing diversity of natural enemies may not benefit the provision of pest control services across landscapes. However, to date, the relative contributions of different natural enemies to pest control, and the strength and direction of their interactions, have almost exclusively been investigated at small spatial and temporal scales (Schmidt et al., 2003; Cardinale et al., 2006; Duffy et al., 2007). Despite their importance for predicting the outcome of ecosystem functioning, the variability of these effects in real-world landscapes is largely unknown.

Moreover, theoretically, an understanding is lacking of whether and why the outcome for prey of interactions between predators may be affected by the landscape context. Despite abundant research on the spatial dynamics of interactions between predators and prey, efforts have mainly focussed in recent years on the importance of the spatial context for food web stability and persistence (Amarasekare, 2008; Abrams et al., 2012). In contrast, to our knowledge, no study has theoretically explored the consequences of a trophic interaction such as intraguild predation for densities of the shared prey, across gradients in landscape complexity. In non-spatially explicit systems, intraguild predation is commonly predicted to lead to a release of the shared prey, due to pressure by top predators on the intermediate, generally more efficient mesopredators (Holt and Polis, 1997). In spatially explicit systems, mechanisms such as the use of alternative prey or spatial refuges from predation are predicted to stabilize and enable the persistence of top and mesopredators (Holt and Huxel, 2007; Abrams et al., 2012). However, empirically, trophic cascades involving release of the shared prey by intraguild predation are found in some (Vance-Chalcraft et al., 2007), but not in all cases (Mooney et al., 2010; Mäntylä et al., 2011), and a theoretical basis for these differences in spatially explicit systems is currently missing (Mooney et al., 2010).

This thesis

The overarching objective of this thesis is to shed light on the mechanisms determining biological pest control at the landscape scale, and thereby improve our ability to predict and manage this service in agricultural landscapes. Given previous knowledge, the following axes are investigated:

In **Part 1**, the aim is to clarify the relationship between landscape context and the provision of pest control. In a field exclusion experiment replicated across a gradient in landscape complexity, the trophic interactions between three functional guilds of natural enemies, and their respective contributions to pest control across landscapes, are disentangled and quantified. Control of two major types of arthropod crop pests is considered: lepidopteran larvae (**Chapter 2**) and aphids (**Chapter 3**). These chapters test the hypothesis that landscape-wide pest control is determined by the combination of 1) interactions occurring between groups of natural enemies, and 2) underlying densities of pest populations, and that the outcome of these effects for final pest control varies according to the landscape context. By experimentally unraveling the contributions to control and the interactions of different enemy guilds independently of pest densities, Part 1 aims to increase our understanding of what factors determine pest control at the landscape scale.

Whereas Part 1 explores pest control provision given natural enemy availability, **Part 2** (**Chapter 4**) delves deeper into what aspects of landscape context and local management determine enemy availability. Natural enemy abundance and species richness benefit from high proportions of seminatural habitat around fields. However, other landscape characteristics such as habitat diversity and configuration may have contrasting effects, and the importance of these parameters may vary across spatial scales. Part 2 tests these hypotheses for seven different natural enemy taxa by disentangling the relative importance of landscape composition, diversity and configuration, and of their interactions with local management intensity, across a range of spatial scales. By gaining a more precise knowledge of what factors affect which enemies, and at what scale, Part 2 aims to increase our ability to effectively manage natural enemy communities for improved pest control in agricultural landscapes, given the contributions to control and the potential interactions, explored in Part 1, of different natural enemy taxa.

Lastly, **Part 3** (**Chapter 5**) expands on previous empirical results by exploring landscape-scale pest control mechanisms in a theoretical model. Based on results of Martin et al. (2013) (Chapter 2), this model aims to test the hypothesis that the outcome for pests of intraguild predation between natural enemies varies according to the landscape context, and to uncover the causes of such variation. Building on results of Part 2, this hypothesis is explored along the two separate axes of habitat amount and configuration, measured by the number and degree of autocorrelation of habitat patches. This model builds on previous food web and intraguild predation theory, and expands it to spatially explicit systems, thereby aiming to develop mechanistic hypotheses and recommendations for management of landscape-scale trophic interactions and their outcome for final pest control.

The project

This thesis was performed within the framework of the Bayreuth Center of Ecology and Environmental Research (BayCEER) international research training group TERRECO: Complex Terrain and Ecological Heterogeneity, funded by the Deutsche Forschungsgemeinschaft. This project is a cooperative research and training effort between the University of Bayreuth (Germany) and several universities and institutions of South Korea, and involved the close collaboration of ca. twenty international professors and PhD students for overall definition of research goals and joint study designs. The aim of this project is to assess the provision and potential for optimization of multiple ecosystem services provided by mountainous landscapes, which are particularly important for their role in water provisioning of much of the world´s population (Liniger et al., 1998). Sustainable stewardship of these landscapes, e.g. by avoiding leaching and run-off of agricultural pollutants, including pesticides, into hydrological pathways, is the overarching objective, aimed at through the integration of research on soils, water yield and water quality, agricultural and forest production, biodiversity, economic yields and losses, stakeholder perceptions, and available institutional structures. The outcome of this project aims to provide stakeholders with decision-making tools that integrate multiple ecosystem services and management scenarios.

1.2. Materials and Methods

1.2.1. Study area

Empirical data collection for this thesis thus took place simultaneously with the measurement of other ecosystem services, in the hydrological catchment of Haean-Myeon, Kangwon Province, in north-eastern South Korea (long. 128°5’ to 128°11’E, lat. 38°13’ to 38°20’N; Figure 1.1). This ca. 62 km^2 region is composed of a 55 km^2 bowl-shaped agricultural landscape (mean altitude 500 m a.s.l.), surrounded by a quasi-uninterrupted chain of forested mountains (Figure 1.2). It forms a major part of the Soyang Lake watershed, the largest freshwater reservoir of South Korea (Park et al., 2010). The Haean catchment is also a major hotspot for Korean agriculture, which strongly impacts the trophic state of the reservoir (Park et al., 2010). Agriculture in this region is largely composed of a mixture of dry annual crops, mainly soy bean, potato, daikon radish and cabbage, and irrigated rice fields concentrated near the center of the catchment. These crop fields (on average <4 ha) are interspersed with a multitude of seminatural margins, one to two-year-old fallows, secondary regrowth, gallery forests and patches of older-growth deciduous forest, which contribute to overall high heterogeneity of the landscape.

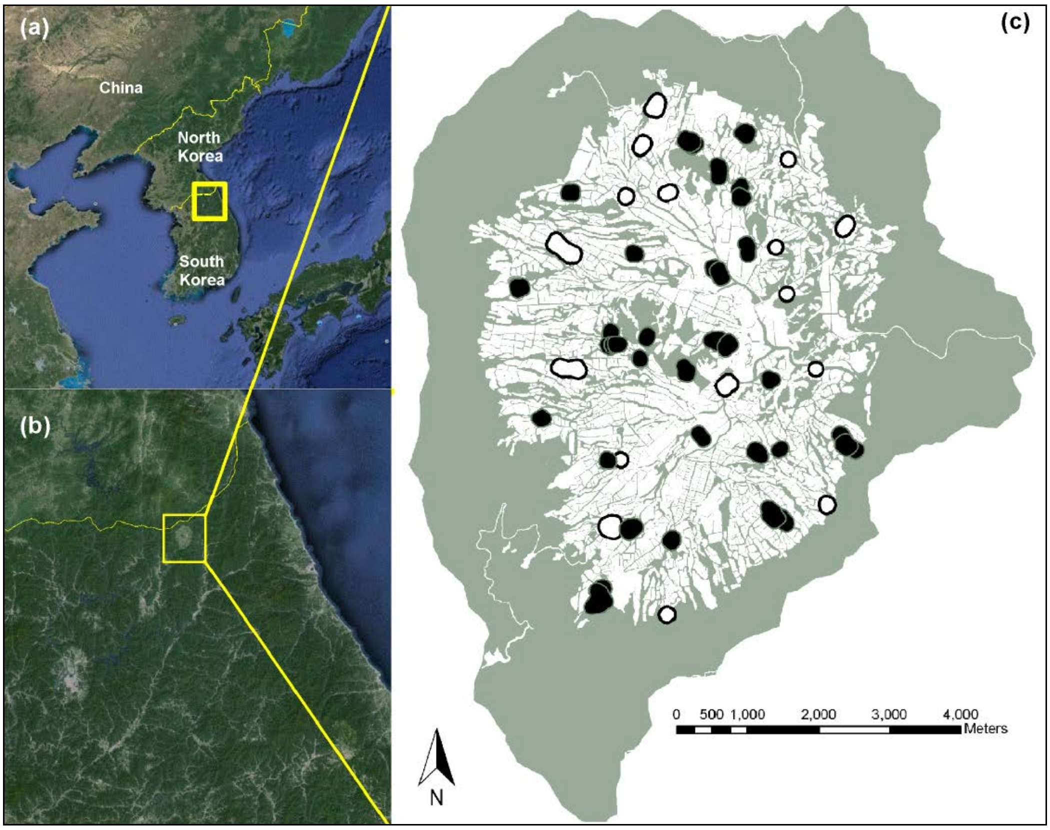

Figure 1.1. Location of the Soyang Lake watershed (a) and the Haean catchment (b) on the north-eastern border of South Korea. Focal agricultural fields within the catchment were selected for experiments in 2009 (Part 2; black marks) and 2010 (Part 1; white marks). Markings show 100 m buffers around fields (c).

Figure 1.2. The Haean landscape and surrounding mountains, photographed from the south-western edge of the catchment.

1.2.2. Part 1: experimental exclusion of natural enemies across a gradient in landscape complexity

In 2010, 18 sites separated by at least 600 m were selected in this region (except 2 sites located 20 km to the south, separated by only 210 m; Figure 1.1). These sites varied in the degree of landscape complexity, measured as the proportion of seminatural habitat in a 300 m radius around fields. In a corner of each site, 20 m ² areas were cordoned off and planted with cabbage *Brassica oleracea* var. *capitata*. Six treatments were installed in these areas, each on four cabbage plants, in order to exclude combinations of three functional guilds of natural enemies: birds (and other vertebrates larger than 1.5 cm), flying insects (syrphids, parasitoid and predatory wasps) and ground-dwellers (spiders, carabid and staphylinid beetles) (Figure 1.3). At the start of the experiment, each treatment was inoculated with a standard number of herbivores (Lepidopteran larvae and aphids) per plant, defined by the mean herbivore density in open treatments of the same plot. An additional treatment excluding enemies and herbivores controlled for abiotic differences between sites. The experiment ran from July to September 2010, during which time arthropods were monitored within the treatments at three occasions (10 day intervals). At the end of the experiment, treated cabbages were harvested and measured for herbivory and total fresh biomass. Data on pest densities, crop herbivory and final biomass were analyzed as a function of landscape complexity using (generalized) mixed effects models in packages nlme (Pinheiro et al., 2013) and glmmADMB (Bolker et al., 2012) with R Statistical Software 2.13.1 (R Development Core Team, 2011).

Figure 1.3. Experimental exclusion cages for combinations of natural enemies, in one of 18 sites. All cages of a given site are initialized with the same number of herbivores. Treatments are: *-G-B-F* (control; exclusion of all enemies), *-G-B* (exclusion of ground-dwellers and birds, but not flying insects), *-F-B* (exclusion of flying insects and birds), *-B* (exclusion of birds), *-G* (exclusion of ground-dwellers), *O* (open, no exclusion).

1.2.3. Part 2: sampling of natural enemies according to local and landscape factors

In 2009, 35 crop fields were selected in the Haean catchment, representing equal proportions (eight fields) of the four major crops: potato, daikon radish, soy bean or rice, as well as three additional fields of cabbage (Figure 1.1). Within a given crop, half of the fields were conventional, and half were organic (except cabbage fields: only conventional management). Fields varied 1) in the amount of seminatural habitat surrounding them (landscape composition); 2) in the complexity of patch shapes, measured by the mean perimeter-area ratio of patches within a radius around fields (landscape configuration); 3) in the diversity of surrounding land cover types, measured as Shannon´s index of habitat diversity (landscape diversity). These parameters were correlated neither with each other nor with local management when measured at scales from 100 m to 1000 m radii around fields (100 m intervals).

Sampling of natural enemies was performed in these fields using pan traps (for syrphids, parasitoids and predatory wasps; on average six 24-hr censuses per field), and in subsets of fields using pitfall traps (for spiders, carabid and staphylinid beetles; on average two 10-day censuses per field) and bird point counts (on average three censuses per field). Three pan trap clusters and five pitfall traps were installed in each field at a gradient of distance from the edge, except in irrigated rice fields where pitfall traps were instead placed along the field edge (Figure 1.4). Rates of herbivory and final crop biomass were measured in a subset of plots. Collected insects were preserved in 82% ethanol and identified to species or morphospecies, and to family level for Parasitica. The abundance and species richness of separate enemy taxa was analyzed at all spatial scales from 100 m to 1000 m around fields (100 m intervals) as a function of 1) local management intensity (organic vs. conventional), 2) landscape composition, configuration and diversity, and 3) the interaction between local management and landscape composition, configuration and diversity, respectively, using mixed effects models in package lme4 (Bates et al., 2013) with R Statistical Software 2.15.1 (R Development Core Team, 2011).

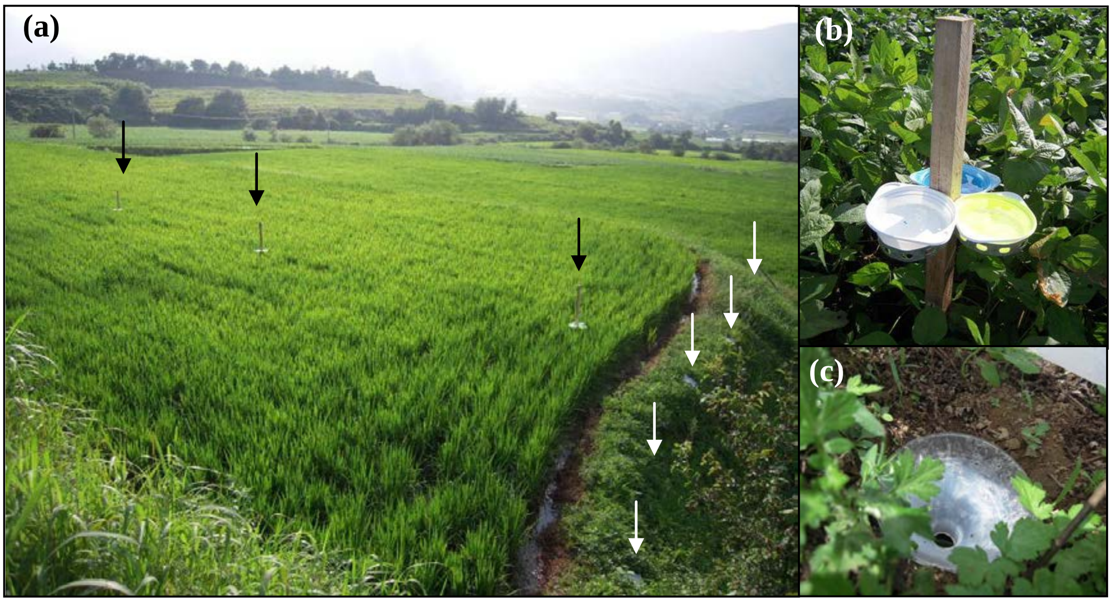

Figure 1.4. Sampling design in one of eight irrigated rice fields (black arrows: pan traps; white arrows: pitfall traps) (a) and detail of pan (b) and pitfall traps (c). Pan traps are filled with water and a few drops of surfactant. Pitfall traps contain 1:3 ethylene glycol (antifreeze) and water.

1.2.4. Part 3: modeling of intraguild predation in a spatial context

A system of stochastic equations was used in R Statistical Software 2.15.1 to model the population dynamics of prey, meso- and top predators in a spatially explicit system inspired by Martin et al. (2013) (Chapter 2). The trophic network considered is one of coincidental intraguild predation, in which top predators (birds) prey on herbivores (pest caterpillars), which may or may not happen to be parasitized by a mesopredator (parasitoid wasp). Top and meso-predators are assumed to persist in this system because of the availability of alternative prey for top predators, which also forage widely in the landscape, and because refuges and spatial structures are available for persistence and recolonization of patches by mesopredators (Holt and Huxel, 2007; Abrams et al., 2012).

The populations of herbivores and mesopredators are modeled directly, using a stochastic logistic growth model (Hassell, 1975) assuming limited but stable resources for herbivores, and a Holling type II functional response to the number of prey (Holling, 1959) for mesopredators, respectively. In contrast, populations of top predators are considered independent of prey and mesopredator densities, and are modeled simply as a mortality rate for herbivores and mesopredators.

These dynamics are modeled in a spatially explicit, fragmented landscape generated in R package ecomodtools (Chipperfield et al., 2011). This landscape contains two types of habitat: agricultural, which contains the resources (crop plants) that herbivorous larvae feed upon, and seminatural, containing floral resources necessary for adult butterflies. Seminatural habitat is considered unsuitable for herbivores, but its proximity determines the fertility of adults. The growth rate of herbivores in a given agricultural patch is thus defined as a linear function of the number of seminatural habitat patches in its immediate neighbourhhood.

1.3. Results and discussion

1.3.1. Natural enemy interactions constrain pest control in complex agricultural landscapes (Chapter 2)

Exclusion of all or combinations of natural enemies from cabbage plants along a landscape complexity gradient impacted the number of larvae of pest Lepidoptera, associated herbivory rates (leaf damage), and final crop biomass. On average for all sites, exclusion of all natural enemies increased the densities of pest larvae by ca. 43%, herbivory by ca. 54%, and decreased crop biomass by ca. 57%. When considered along a landscape complexity gradient, in the absence of natural enemies, pest larval density and herbivory were found to increase, and biomass to decrease, with the proportion of seminatural habitats around fields. However, when all but flying insect enemies were excluded, these responses did not vary across landscapes. As a result, flying insect enemies appeared to reduce pests by only 1 larva per exclosure, and herbivory by 0.8%, in simple landscapes with little seminatural habitat, but by 11 larvae per exclosure and 37%, in complex landscapes with high amounts of seminatural habitat.

In contrast, effects of enemy guilds including birds did not increase with landscape complexity, and were weaker in complex landscapes than with flying insects alone (only ca. 12% herbivory reduction compared to ca. 37%). Birds thus appeared to constrain the effects of flying insect enemies on pests in complex landscapes, indicating the presence of a negative interaction between these two guilds. However, in simple landscapes, pest control was stronger (ca. 5.4%) in the presence of birds and flying insects, than with with flying insects alone (ca. 0.8%), thus birds appeared to have a direct positive impact on pest control in simple landscapes.

Contrary to birds, interactions between ground-dwellers and flying insects did not impact overall control of these pests.

Similar patterns were found for pest densities, herbivory rates and less significantly for final crop biomass. In complex landscapes, flying insects alone accounted for a ca. 6.1-fold increase in biomass compared to controls without enemies, whereas this increase was only 2.6-fold in the presence of all enemies. A trophic cascade involving natural enemy interactions thus took place that impacted all levels from pests, to crop damage, to yields, and the outcome of this cascade for final pest control was landscape-dependent.

Mechanisms leading up to negative interactions between birds and flying insects in complex landscapes may include intraguild predation (IGP) and / or behavioural interference. As insectivorous birds are known to consume both adult insects and caterpillar larvae, predation by birds of either adult wasps (omnivorous IGP) or parasitized caterpillars (coincidental IGP) is likely to explain the pattern of herbivore release observed in complex landscapes. However, based on empirical results alone and available theory, it remains unclear what causes this pattern to change from complex to simple landscapes. This question is thus further explored in the following paragraphs (1.3.4: Chapter 5).

Importantly, this experiment demonstrates that trophic interactions have variable impacts on ecosystem function across landscapes. Effects of natural enemies on crop damage and yields are thus not deducible from patterns of natural enemy diversity only, but need to take into account both underlying pest distributions, and the potential interactions of multiple enemy species and functional groups. According to these results, flying insects including mainly parasitoid and predatory wasps have the strongest potential to control populations of Lepidopteran pests, under conditions of high landscape complexity, and defining appropriate habitat management schemes that promote flying insects while avoiding negative interactions is key to improving biological pest control across landscapes.

1.3.2. Pest control of aphids depends on landscape complexity and natural enemy interactions (Chapter 3)

Effects of natural enemy exclusion on aphid pest control across landscapes were different from those on Lepidopteran control. On average across sites and sampling rounds, aphids were reduced ca. 77% by all natural enemies combined, compared to controls excluding all enemies. Similarly to Lepidopteran larvae, when considered across a landscape complexity gradient, aphid densities in the absence of natural enemies increased ca. 5.5±2.6-fold from simple to complex landscapes. However, in the presence of all natural enemies combined, aphids were reduced to similar densities in all landscapes. As a result, suppression of aphid pests by all natural enemies increased ca. 6±2.5-fold with landscape complexity.

In addition, this suppression was stronger in open treatments accessible to all enemies, than in treatments excluding particular functional guilds. In particular, the separate effects of ground-dwellers and flying insect enemies were less strong across landscapes than those of both these guilds combined, indicating an overall complementary interaction between these enemies that was maintained across the gradient in landscape complexity. Individual effects of flying insects, however, increased more strongly with landscape complexity than effects of ground-dwellers only, and in the most complex landscapes, flying insects reduced aphids 1.4 to 2 times more than ground-dwellers did. Although parasitism rates were lower in the presence of ground-dwellers than without them, indicating possible intraguild predation of parasitized aphids by ground-dwellers and thus a sub-additive interaction between these guilds, this interaction did not hinder the overall complementary of ground-dwellers and flying insects for aphid suppression.

Overall, bird exclusion did not appear to influence aphid suppression. However, parasitism rates and syrphid:aphid ratios indicate that interactions took place that did not translate into detectable differences in pest densities. Parasitism and syrphid:aphid ratios were lower in the presence of birds than without them, suggesting that birds preyed on parasitized mummies and on syrphids in addition to aphids, which may have had opposing effects of aphid reduction and release by intraguild predation. Interestingly, effects of birds on syrphids were not found in the presence of ground-dwellers, which by acting as alternative prey these generalist predators may have released bird predation pressure on other enemies.

In agreement with stronger effects of flying insects in complex than in simple landscapes, aphid population growth was lower in complex than in simple landscapes, and was negatively correlated with parasitism and syrphid:aphid ratios. Syrphid densities were also positively related to final crop biomass, indicating that particularly in complex landscapes, flying insects had a direct positive impact on both pest suppression and final yields.

This study shows that the outcome of natural enemy interactions across landscapes may vary within the same system according to the type of pest organism considered. In contrast to Lepidoptera, aphid pest control increased overall with landscape complexity and was not significantly hindered by interactions occurring between natural enemy guilds: rather, the overall impacts of multiple guilds were complementary across landscapes. As in the case of Lepidoptera, flying insect enemies were most effective at suppressing aphid populations, particularly under conditions of high landscape complexity. Positive effects of landscape complexity on pest control by flying insects and other guilds are in agreement with its generally positive effects on natural enemy abundance and species richness (e.g., Tscharntke et al., 2012). By showing under what spatial conditions, and for which pests and enemies, higher enemy diversity actually benefits pest control, this experiment provides a functional backdrop of predictions for the consequences of increased landscape-scale enemy diversity. It shows that improving pest control at the landscape scale may depend on careful selection of management measures that increase effects of some enemies, while avoiding negative interactions with others, and this at all the spatial scales relevant to the activity of enemy organisms. In this context, consideration of “landscape complexity” as an overarching factor characterized by correlated components of habitat composition, diversity and configuration, is not sufficient to identify relevant management guidelines, which thus further require disentanglement of the separate effects, and relative importance, of distinct landscape parameters for the diversity of multiple natural enemy groups across scales.

1.3.3. Scale-dependent effects of landscape composition and configuration on the natural enemies of insect pests (Chapter 4)

Exploration of the separate effects of landscape composition, configuration and diversity on the abundance and species richness of natural enemies across scales yielded unexpected results. Instead of the amount of seminatural habitat around fields, which is the most widespread measure of landscape complexity in previous studies of enemy diversity (Chaplin-Kramer et al., 2011), a complex configuration of habitats around fields had the most consistently positive effect on natural enemy groups across spatial scales. This was found for the species richness and abundance of syrphids, predatory wasps, parasitoids (i.e., all flying insects) and staphylinids, as well as for bird species richness in conventional fields, but not for their abundance. Carabids, however, were not affected by landscape configuration, and spiders did not respond to any landscape parameter at the scales tested.

In contrast, of all seven taxa, only carabids responded positively to the amount of habitat around fields, and parasitoid wasps even showed a consistently negative response to this parameter across scales. In previous studies of natural enemy diversity, parameters of landscape composition (amount of habitat) and configuration (shape of habitat patches) are rarely distinguished from each other, as fine-grained landscapes frequently also contain the highest amounts of habitat. According to our results, previously observed positive effects of landscape complexity may have been driven by the configuration of habitats instead of their amount. This result is in line with studies that distinguish these factors at one to two landscape scales, which show stronger effects of habitat configuration than composition on several taxa (Schweiger et al., 2005; Hendrickx et al., 2007; Bailey et al., 2010). The implications of this difference are considerable, as managing landscapes for small, complex-shaped fields interspersed with seminatural margins is thus shown to be more beneficial to enemies, and particularly to flying insects, than reducing the total area of productive cropland in favor of less productive natural or seminatural habitat. Interestingly, at the scales tested, the positive effects of landscape configurational complexity on flying insects did not apply to bird abundance. In light of previously described mechanisms (1.3.1), managing this parameter thus holds the potential to improve landscape-scale pest control while avoiding negative interactions between guilds.

Tests of these factors at multiple spatial scales confirmed the robustness of results, as the contrasting effects of landscape configuration and composition were maintained across all scales from 100 m to 1000 m around fields. In addition, the strength or slope of these effects was found to generally increase with spatial scale. In contrast to landscape composition and configuration, effects of landscape diversity were observed mainly at larger scales above 700 m, with positive or negative impacts according to taxa. Even within taxa, the relative impact of these three landscape parameters thus depended on the spatial scale considered, leading to the corollary that effects at a range of scales potentially relevant to organisms need to be investigated, in order to ascertain when and how different enemies are affected by the landscape structure.

Different taxa were best predicted by different scales, depending on their mobility and body size. Ground-dwellers, and the very small parasitoid wasps, were best predicted by models at small scales (300-400 m), whereas larger and further ranging predatory wasps, syrphids and birds were best predicted by large scales (800-900 m). However, as described above, significant effects with consequences for landscape management were found at all tested scales, and are likely to be present at even larger scales not measured here (Thies et al., 2003). Restricting analyses to most predictive scales would thus not take into account the variability of effects within taxa across scales, and thus would limit our ability to manage natural enemy communities across whole landcapes.

Finally, interactions between landscape factors and local management intensity occurred only rarely for these taxa and scales. Organic management improved the abundance and/or richness mainly of flying insects (parasitoids, syrphids and non-significantly predatory wasps) compared to conventional management, and this effect was independent of the landscape context. Local and landscape factors interacted at more than two successive scales only in the case of birds, whose species richness increased more strongly with landscape configuration and diversity in conventional compared to organic fields, in agreement with recently formulated hypotheses stating that higher landscape complexity should benefit organisms more in intensively managed areas than in extensive ones (Concepción et al., 2012; Tscharntke et al., 2012).

1.3.4. Intraguild predation in a spatial context: the influence of landscape heterogeneity (Chapter 5)

Following the experiment of Chapters 2 and 3, one question in particular remained unanswered: what may have caused the outcome of natural enemy interactions for pests to change across a gradient in landscape complexity?

In this chapter, empirical results are used as a basis for a theoretical model explaining this mechanism. In a first step, simulation of the population dynamics of mesopredators and prey, in the presence or absence of a vertebrate top predator, showed that intraguild predation, even coincidental, may indeed lead to different outcomes for the prey according to the landscape structure. In landscapes with high amounts of seminatural habitat and low autocorrelation (high configurational complexity), vertebrate top predators such as birds caused a release of the shared prey (herbivores), in accordance with previous intraguild predation theory (e.g., (Holt and Polis, 1997). However, in landscapes with little seminatural habitat or high autocorrelation, these effects were inverted, and top predators led instead to a decrease of the shared prey, compared to effects of mesopredators (parasitoids) only.

In a second step, investigation of the population variability of mesopredators and prey showed that in certain landscapes, top predators have stabilizing effects on the dynamics of mesopredators and prey, and this leads to top predators causing herbivore reduction instead of release. In landscapes with only few or distant resources for adult herbivores (little seminatural habitat or high autocorrelation), populations of herbivores and mesopredators are unstable, and local extinction rates of mesopredators are high. Addition of a vertebrate top predator in these systems, whose dynamics do not depend on local resources, stabilizes mesopredator-prey populations by reducing mesopredator extinction rates. As a result, pressure on herbivores increases.

In contrast, in landscapes with high amounts of habitat and low autocorrelation, herbivores are a stable and abundant resource for mesopredators, who exhibit low rates of local extinction. Adding top predators to this already stable system leads to mesopredator reduction and, ultimately, to herbivore release.

These results thus confirm the empirical findings of Chapter 2. In addition, they provide a theoretical framework explaining the discrepancy between theory, and empirical observations of the effects of vertebrate top predators, which are often found to reduce prey in local studies instead of releasing it (Mooney et al., 2010). According to these results, in situations with a high potential for negative intraguild predation interactions between enemies, top predators will benefit prey reduction when mesopredators are locally unstable relative to top predators, but will release the shared prey when mesopredators are stable. Measurement of the turnover dynamics of different trophic levels across large spatial as well as temporal scales may thus yield important insights into the outcome of species interactions for ecosystem functioning, and provide valuable indications for pest control management in agricultural landscapes.

1.4. Conclusions

This thesis shows that provision of pest control services at the landscape scale depends on the nature and strength of interactions between natural enemies, and that these may vary according to the landscape context. Optimizing landscapes for pest control thus implies rigorous management of different landscape parameters at multiple scales, in order to selectively influence natural enemy communities according to their effectiveness and the trophic interactions of functional groups.

Landscape configuration was found to be a major factor influencing the diversity of enemy taxa at multiple scales, in comparison to only few effects of landscape composition (amount of seminatural habitat). This factor was particularly important for the abundance and species richness of flying insect enemies, including syrphids, parasitoids and predatory wasps, which also showed the strongest potential for control of Lepidopteran and aphid pests under conditions of high landscape complexity, and in the absence of negative interactions with other guilds.

In the absence of predation by natural enemies, underlying densities of herbivorous pests increased with the amount of seminatural habitat around fields. This increase was found for two major groups of pests and in both empirical and theoretical approaches. Pests may thus generally benefit from landscape complexity, but their final, observed distribution across landscapes depends on the strength of pest suppression by entire communities of natural enemies.

Importantly, more enemies do not necessarily lead to fewer pests. Because the effects of enemy diversity change across landscapes, pest control cannot be predicted from enemy diversity alone. Consequently, biodiversity – ecosystem functioning relationships based on networks of trophic interactions are landscape-dependent. Variable outcomes of enemy diversity for landscape-scale pest control are shown here to depend upon the turnover dynamics of interacting predators and prey, and on the differences in spatial and temporal scales experienced by multiple predator populations.

Lastly, this thesis provides insight into the value of addressing multiple scales for biodiversity within a landscape. It shows that the relative importance of different landscape parameters on biodiversity varies according to scale independently of the most predictive scales of response, and that the simultaneous effects of landscape context at multiple scales need to be taken into account for management of biodiversity in agricultural landscapes.

1.5. Manuscripts in this thesis and individual contributions

The studies described in this thesis refer to the following four manuscripts. Manuscript 1 is published in *Proceedings of the National Academy of Sciences of the USA* (Chapter 2). Manuscript 2 is submitted to the *Journal of Applied Ecology* (Chapter 3). Manuscripts 3 and 4 are *in preparation* (Chapters 4 and 5).

Manuscript 1 (Chapter 2)

Title	Natural enemy interactions constrain pest control in complex agricultural landscapes
Authors	Emily A. Martin, Björn Reineking, Bumsuk Seo, Ingolf Steffan-Dewenter
Journal	*Proceedings of the National Academy of Sciences of the USA*
Status	published

Author contributions

E.A. Martin	Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)
B. Reineking	Analysis, discussion, manuscript editing
B. Seo	Data collection
I. Steffan-Dewenter	Design, discussion, manuscript editing

Manuscript 2 (Chapter 3)

Title	Pest control of aphids depends on landscape complexity and natural enemy interactions
Authors	Emily A. Martin, Björn Reineking, Bumsuk Seo, Ingolf Steffan-Dewenter
Journal	*Journal of Applied Ecology*

Status	submitted

Author contributions

E.A. Martin	Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)
B. Reineking	Analysis, discussion, manuscript editing
B. Seo	Data collection
I. Steffan-Dewenter	Design, discussion, manuscript editing

Manuscript 3 (Chapter 4)

Title	Scale-dependent effects of landscape composition and configuration on natural enemy diversity and biological pest control
Authors	Emily A. Martin, Bumsuk Seo, Chan-Ryul Park, Björn Reineking, I. Steffan-Dewenter
Status	in preparation

Author contributions

E.A. Martin	Design, methods, data collection, analysis, discussion, manuscript writing and editing (corresponding author)
B. Seo	Data collection
C.-R. Park	Data collection
B. Reineking	Discussion, manuscript editing
I. Steffan-Dewenter	Design, discussion, manuscript editing

Manuscript 4 (Chapter 5)

Title	Intraguild predation in a spatial context: the influence of landscape heterogeneity
Authors	Emanuel Fronhofer, Emily A. Martin
Status	in preparation

Author contributions

E. Fronhofer	Design, discussion, modeling, manuscript writing and editing (methods, results)
E.A. Martin	Design, discussion, manuscript writing and editing (introduction, discussion) (corresponding author)

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Part 1

Chapter 2

2. Natural enemy interactions constrain pest control in complex agricultural landscapes

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Abstract

Biological control of pests by natural enemies is a major ecosystem service delivered to agriculture worldwide. Quantifying and predicting its effectiveness at large spatial scales is critical for increased sustainability of agricultural production. Landscape complexity is known to benefit natural enemies, but its effects on interactions between natural enemies and the consequences for crop damage and yield are unclear. Here we show that pest control at the landscape scale is driven by differences in natural enemy interactions across landscapes, rather than by the effectiveness of individual natural enemy guilds. In a field exclusion experiment, pest control by flying insect enemies increased with landscape complexity. However, so did antagonistic interactions between flying insects and birds, which were neutral in simple landscapes and increasingly negative in complex landscapes. Negative natural enemy interactions thus constrained pest control in complex landscapes. These results show that by altering natural enemy interactions, landscape complexity can provide ecosystem services as well as disservices. Careful handling of the tradeoffs between multiple ecosystem services, biodiversity and societal concerns is thus crucial, and depends on our ability to predict the functional consequences of landscape-scale changes in trophic interactions.

Keywords

Arthropods and birds; biodiversity-ecosystem functioning; biological pest control; ecosystem service provision; land use intensification.

2.1. Introduction

Globally, approximately 10% of agricultural yields are estimated to be destroyed by animal pests before harvest (Oerke, 2006), despite intensive measures of crop protection including the widespread use of chemical pesticides. Although chemical pesticide use has increased 15 to 20-fold in the past 40 years, estimated crop losses to pests have also significantly increased (Oerke, 2006), and the successful control of pests by naturally occurring biological agents is of key economic and ecological importance (Lewis et al., 1997; Losey and Vaughan, 2006). The natural enemies of insect pests are responsible for an estimated 50 to 90% of the biological pest control occurring in crop fields (Pimentel, 2005). In landscapes containing large amounts of natural or seminatural habitat, natural enemies are often more diverse and abundant than in structurally simple, intensely cultivated landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). As a result, biological pest control is expected to be higher in complex than in simple landscapes (Thies and Tscharntke, 1999; Chaplin-Kramer et al., 2011), and may efficiently replace control by pesticides (Thies and Tscharntke, 1999). However, two elements may alter the relationship between landscape structure and the provision of biological control. Firstly, the contribution of natural enemies to pest control across landscapes depends on the spatial variability of the pests themselves, and knowledge of how much damage would occur in the absence of enemies is a prerequisite (Gardiner et al., 2009; Chaplin-Kramer et al., 2011). Secondly, biological control is not only a result of enemy diversity and abundance, but also of the trophic interactions occurring between enemies (Schmidt et al., 2003; Duffy et al., 2007; Thies et al., 2005; Tylianakis et al., 2007; Straub et al., 2008; Tscharntke et al., 2012). If these vary according to the landscape context, then understanding ecosystem service variability requires understanding the variations of trophic interactions at multiple spatial scales (Loreau et al., 2003; Knight et al., 2005; France and Duffy, 2006; Carpenter et al., 2009; Tylianakis and Romo, 2010; Tscharntke et al., 2012).

Several local studies of the link between diversity and ecosystem function indicate that trophic interactions between diverse enemy assemblages may lead to potentially negative, neutral or positive consequences for ecosystem functioning and service provision (Schmidt et al., 2003; Finke and Denno, 2004; Straub et al., 2008; Tylianakis and Romo, 2010). The direction of these responses depends on the type of interaction occurring between enemy species or functional groups, which may be antagonistic, neutral, additive or synergistic and involve intraguild predation, functional redundancy, niche partitioning or facilitation, respectively (Schmidt et al., 2003; Finke and Denno, 2004; Straub et al., 2008). In contrast, little is known about the role of landscape context in determining trophic interactions and their consequences for ecosystem service provision (Loreau et al., 2003; Carpenter et al., 2009; Mooney et al., 2010; Mäntylä et al., 2011), despite the documented importance of landscapes in regulating species functional diversity (Luck and Daily, 2003; Bianchi et al., 2006; Harvey et al., 2006; Chaplin-Kramer et al., 2011; Rand et al., 2012). Given the implications for landscape-wide effectiveness of biological control and other biodiversity-dependent services, scaling up the interaction mechanisms of functional species groups to a landscape perspective is critical for the development of sustainable management strategies (Carpenter et al., 2009; Daily et al., 2009; Chaplin-Kramer et al., 2011; Tscharntke et al., 2012) as well as for increased predictability of ecosystem functioning (Loreau et al., 2003; France and Duffy, 2006; Duffy et al., 2007; Tylianakis and Romo, 2010; Tscharntke et al., 2012).

In a field exclusion experiment, we investigated the effects of landscape complexity on the trophic interactions between natural enemies of insect pests, by measuring the separate and combined contributions to biological pest control of three functional groups of natural enemies, namely birds, flying insects and ground-dwelling arthropods. In 18 experimental plots of a South Korean agroecosystem, six insect and bird exclosure treatments were installed each around four plants of cabbage (*Brassica oleracea* var. *capitata*; Figure S2.1). Exclosures restricted access to the plants by none, single or combinations of the three natural enemy guilds. Initial densities of herbivores, particularly larvae of the native Lepidoptera *Pieris rapae*, *P. brassicae* (Linné) and *Trichoplusia ni* (Hübner), were standardized between exclosures using average densities of non-treated plants. Using linear and generalized linear mixed effects models, pest larval densities, the degree of herbivory (leaf damage) and the final biomass of each plant (total n = 432) were compared between exclosure treatments as a function of the landscape context. Complexity of the landscape was measured as the percentage of seminatural habitat at radii from 100 to 1000 m (100 m intervals) around each plot (Thies and Tscharntke, 1999), as seminatural areas represent the main habitat class of interest for agents of pest control in agricultural landscapes. Analyses were restricted to the scale with the best AIC fit (300 m). The strength of enemy contributions to biological control was estimated by differences in pest densities, herbivory rates and biomass compared to controls excluding all enemies (Oerke, 2006; Gardiner et al., 2009).

2.2. Results

On average, treatments accessible to all natural enemies led to 43% lower pest densities, 54% lower leaf damage and 57% higher biomass than controls excluding enemies (Table 2.1, Figure 2.1). Strong differences in pest densities between treatments were reflected by the differences in herbivory rates, showing lower densities and damage in treatments excluding birds, than in those including them (Figure 2.1 A, B). These differences were tempered at the level of yields (Figure 2.1 C). Effects of natural enemy guilds on pest control and yields were influenced, however, by differences at the landscape level. From simple to complex landscapes, pest densities and herbivory rates

Table 2.1. Results of (generalized) linear mixed effects models relating pest larval density, herbivory and biomass to explanatory variables (n = 318 and 432 in 18 plots).

Explanatory variables	nDF	dDF	Test statistic	p
Pest density			Deviance	
Treatment	5	-	53.48	<.0001 ***
% Seminatural habitat	1	-	6.42	0.011 *
Treatment X % Seminatural habitat	5	-	13.46	0.019 *
Herbivory (%)			F	
Treatment	5	80	14.12	<.0001 ***
% Seminatural habitat	1	15	4.9	0.043 *
Management intensity	1	15	5.42	0.034 *
Treatment X % Seminatural habitat	5	80	3.88	0.003 **
Biomass (g)			Deviance	
Treatment	5	-	11.68	0.039 *
% Seminatural habitat	1	-	3.12	0.077 .
Management intensity	1	-	9.64	0.002 **
Treatment X % Seminatural habitat	5	-	15.78	0.008 **

Variables selected by maximum likelihood ratio tests are treatment (six levels of natural enemy exclusion), landscape complexity (% seminatural habitat in a 300 m radius around plots), their interaction, and management intensity of the nearest surrounding field (organic or conventional). nDF: numerator degrees of freedom, dDF: denominator degrees of freedom (significance codes ‘***’ p<0.001, ‘**’ p<0.01, ‘*’ p<0.05).

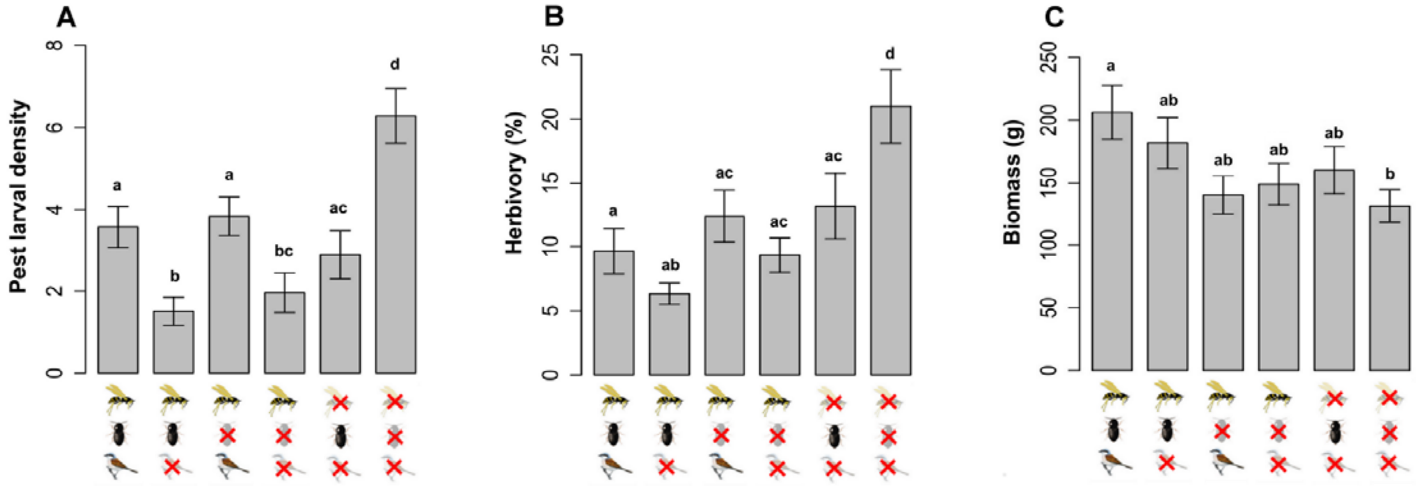

Figure 2.1. Effects of natural enemy exclusion on means ± s.e.m. per treatment. A) Pest larval density (individuals/cage), B) herbivory (%) of individual plants, C) fresh biomass (g) of individual plants. Different letters indicate significant differences among guilds (adjusted p-values <0.05). Effects of landscape complexity and interactions were significant in all cases (Table 2.1; Figures 2.2, 2.3, S2.2). Crossed-out symbols signify exclusion of corresponding natural enemy functional guilds. Treatments remain accessible to non-excluded guilds. Guilds of natural enemies are: flying insects, mainly parasitoids, syrphid flies and predatory wasps (wasp symbol); ground-dwellers, mainly carabid beetles, staphylinids and spiders (beetle symbol); birds and other vertebrates larger than 1.5 cm (bird symbol).

increased, except in treatments excluding birds but not flying insects (Figures 2.2, 2.3, S2.2). As a consequence, the difference between these treatments and controls excluding all enemies increased with landscape complexity. This indicates that the strength of pest control was higher in complex than in simple landscapes mainly for flying insects, which reduced pest densities by ca. 11 larvae/exclosure in complex landscapes and 1 larva/exclosure in simple landscapes, and herbivory by 37% in complex landscapes and 0.8% in simple landscapes ($t = -3.1$, adjusted $p = 0.015$ and $t = -2.74$, adjusted $p = 0.014$ for pest densities and herbivory, respectively; Figures 2.3, 2.4).

In contrast, the effects of ground-dwellers and enemy guilds including birds did not vary significantly with landscape complexity (Figures 2.3, 2.4). The strong effects of flying insects on pest control in complex landscapes were thus constrained by antagonistic interactions with other enemy guilds (Figure 2.4, Table 2.2). In landscapes with >25% seminatural habitat, damage reduction by flying insects was significantly weaker in the presence of birds than in treatments excluding them (Figures 2.4, 2.5). In complex landscapes, the presence of birds reduced the pest control potential of flying insects from ca. 37 to 12% herbivory reduction compared to controls. However, in simple landscapes, herbivory reduction was stronger in the presence of birds (ca. 5.4%) than with flying insects only (ca. 0.8%), indicating that birds played a small direct role in pest control in landscapes with < 25% habitat. In contrast, between ground-dwellers and flying insects, interactions were neutral: combined effects of ground-dwellers and flying insects were not significantly different from the strongest separate effects of these guilds in all landscapes (Figures 2.4, 2.5; Table 2.2).

Pest density followed a similar pattern to herbivory across the landscape gradient (Figure 2.3, Table S2.1). These two variables were also positively correlated (Pearson´s $r = 0.38$, $p < 0.001$). Further, respective exclusion treatments for ground-dweller and flying insect guilds effectively reduced spider densities, rates of parasitism, and rates of predation (Figure S2.3), while bird exclusion tended to increase the activity of flying insects (Figure S2.3). Crop

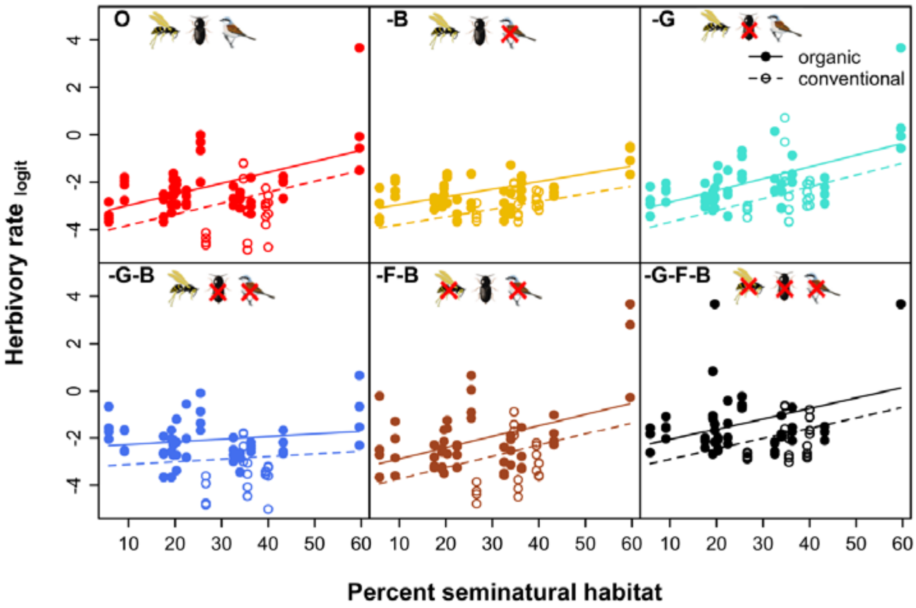

Figure 2.2. Effects of landscape complexity on logit-transformed herbivory in six natural enemy exclusion treatments. Each point represents one cabbage plant (4 plants per treatment and landscape; n=432). Regression lines show predicted model results given organic (full points and solid lines; 13 plots) or conventional (open points and dashed lines; 5 plots) management of the nearest surrounding field (independent covariate; Table 2.1). Natural enemy exclusion treatments are *O*: open treatment without exclusion; *-B*: exclusion of birds; *-G*: exclusion of ground-dwellers; *-G-B*: exclusion of ground-dwellers and birds, but not flying insects; *-F-B*: exclusion of flying insects and birds; *-G-F-B*: control excluding all enemies but including herbivores. See detailed legend description in Figure 2.1. See Figure S2.2 for pest density and biomass results.

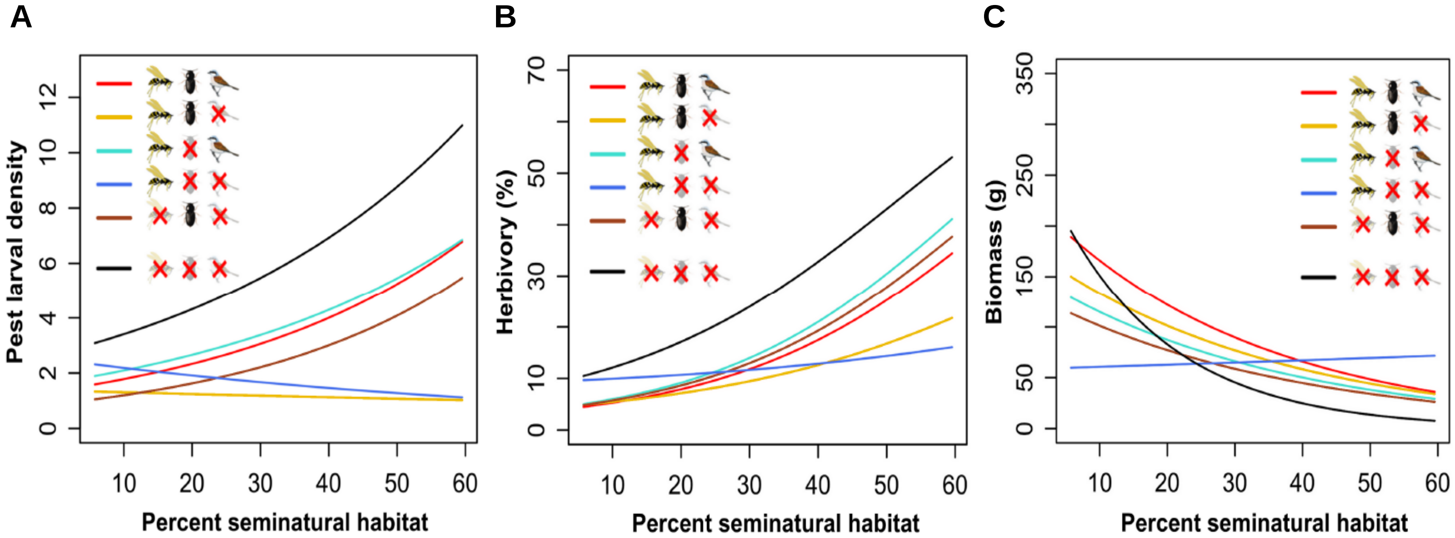

Figure 2.3. Effects of exclusion of natural enemy functional guilds across a gradient in landscape complexity on A) pest larval density, B) herbivory (%), and C) crop biomass (g). Interactions of treatment and % seminatural habitat are significant (Table 2.1). See Tables 2.2 and S2.1 for slope and intercept differences. Lines represent predicted values (backtransformed for herbivory; Methods and Supplementary Methods). Detailed legend description is provided in Figure 2.1.

biomass, as the endpoint of interest for farmers in terms of yield, was also similarly affected by exclusion treatments and landscape complexity (Table 2.1, Figures 2.1, 2.3, S2.2) and was negatively related to herbivory (Pearson´s r = -0.53, p < 0.001). Landscape effects on natural enemy interactions thus led to a trophic cascade affecting all levels from natural enemies, to pest densities and damage, to final crop biomass. Similar results were obtained if habitat diversity instead of % seminatural habitat was used to characterize landscape complexity (Methods, Table S2.2, Figure S2.4). Paralleling herbivory, crop biomass decreased with increasing landscape complexity, except in treatments excluding all but flying insects (Figures 2.3, S2.2). Thus, in a situation without negative interactions with vertebrates, flying insects in complex landscapes could increase the mean crop biomass per plant ca. 6.1 times, instead of ca. 2.6 times in the presence of all enemies. Although effects were less significant for biomass than for herbivory and pest density (Table S2.1), the absolute loss in biomass was high, indicating that effects of enemy interactions had a clear indirect impact on yields.

Herbivory was higher, and resulting crop biomass lower, in plots surrounded by organic than by conventional management (Table 2.1; Figures 2.2, S2.2), but this factor did not impact pest densities. This points to the presence of bottom-up effects through higher N availability near conventional fields, and confirms that pest dispersal into the plots was unaffected by the management intensity of nearby fields.

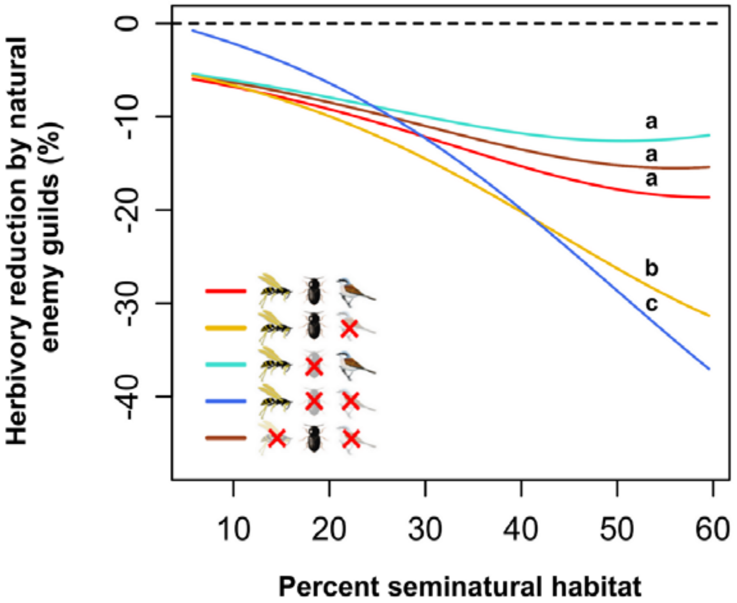

Figure 2.4. Contribution of natural enemy functional guilds to damage reduction across landscapes. Herbivory reduction by natural enemies is compared to no reduction in the absence of enemies. Values represent total reduction of herbivory (%) in the presence of enemies relative to controls without enemies ($Herbivory_{treatment} - Herbivory_{control}$). Differences are based on model predicted values. Different letters indicate significant differences among guilds (adjusted p-values <0.05; Table 2.2).

Table 2.2. Multiple comparisons between enemy contributions to herbivory reduction.

Treatments	Enemy contributions			Value	SE	z	p	p (adjusted)
Slope differences								
-G-B vs. -F-B	🐝	**vs.**	🪲	**-0.036**	**0.011**	**-3.231**	**0.001 ****	**0.005 ****
-G-B vs. -G	🐝	**vs.**	🐦 🐝	**0.038**	**0.011**	**3.445**	**0.001 ****	**0.003 ****
-G-B vs. -B	🐝	vs.	🪲 🐝	0.021	0.010	2.168	0.030 *	0.060 .
-G-B vs. O	🐝	**vs.**	🐦 🪲 🐝	**0.035**	**0.010**	**3.520**	**0.000 *****	**0.003 ****
-F-B vs. -B	🪲	vs.	🪲 🐝	-0.015	0.011	-1.398	0.162	0.259
-F-B vs. O	🪲	vs.	🐦 🪲 🐝	-0.001	0.011	-0.110	0.912	0.912
-G vs. O	🐦 🐝	vs.	🐦 🪲 🐝	-0.003	0.011	-0.309	0.757	0.887
-B vs. O	🪲 🐝	vs.	🐦 🪲 🐝	0.014	0.010	1.465	0.143	0.254
Intercept differences								
-G-B vs. -F-B	🐝	**vs.**	🪲	**0.967**	**0.342**	**2.830**	**0.005 ****	**0.012 ***
-G-B vs. -G	🐝	**vs.**	🐦 🐝	**-0.945**	**0.340**	**-2.782**	**0.005 ****	**0.012 ***
-G-B vs. -B	🐝	vs.	🪲 🐝	**-0.870**	**0.296**	**-2.936**	**0.003 ****	**0.011 ***
-G-B vs. O	🐝	**vs.**	🐦 🪲 🐝	**-1.039**	**0.303**	**-3.428**	**0.001 ****	**0.003 ****
-F-B vs. -B	🪲	vs.	🪲 🐝	0.097	0.330	0.296	0.768	0.887
-F-B vs. O	🪲	vs.	🐦 🪲 🐝	-0.072	0.336	-0.213	0.831	0.887
-G vs. O	🐦 🐝	vs.	🐦 🪲 🐝	-0.094	0.334	-0.281	0.779	0.887
-B vs. O	🪲 🐝	vs.	🐦 🪲 🐝	-0.169	0.289	-0.584	0.559	0.813

Tests are based on the model contrast matrix of herbivory (adjusted p-values: Benjamini-Hochberg method). *-G-B*: exclusion of ground-dwellers and birds; *-F-B*: exclusion of flying insects and birds; *-B*: exclusion of birds; *-G*: exclusion of ground-dwellers; *O*: no exclusion. Statistically significant differences between enemy guilds are indicated in bold (significance codes '***' p<0.001, '**' p<0.01, '*' p<0.05, '.' p<0.1). See Table S2.1 for pest density and biomass results.

2.3. Discussion

In contrast to frequent expectations (Bianchi et al., 2006; Chaplin-Kramer et al., 2011), pressure by herbivores was higher in this study in complex than in simple landscapes. Our data suggest that this may be in part due to a release from control by negative interactions occurring between birds and flying insect enemies. Higher availability of overwintering habitats, alternative resources, and refuges against agricultural disturbance in seminatural habitats may also promote higher pest populations in addition to enemies (Thies et al., 2005). In the absence of negative interactions with other guilds, we show that high rates of control by flying insects occur in complex landscapes (Chaplin-Kramer et al., 2011; Rand et al., 2012), in agreement with their frequently higher densities in complex landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). However, high pest control by flying insects was counteracted by stronger herbivore pressure, thus leading to no differences in herbivory between landscapes in the presence of flying insects only (Thies et al., 2005). Relative to other guilds, flying insects presented the strongest potential for reducing herbivory by pests, under conditions of high landscape complexity (Thies et al., 2005). Their promotion by appropriate habitat management schemes may thus have the strongest potential for improvement of biological control in simple landscapes.

Several mechanisms may explain the patterns observed between guilds of flying insects and birds, assuming the effectiveness of exclosures for other natural enemies (Figure S2.3). Apparent negative interactions between flying insects and birds may indeed be linked with either coincidental or omnivorous intraguild predation (parasitoids consumed indirectly through predation of parasitized herbivores, or direct predation of adult predatory or parasitoid wasps (Straub et al., 2008; Mooney et al., 2010). Given that these interactions directly impact pest densities, and

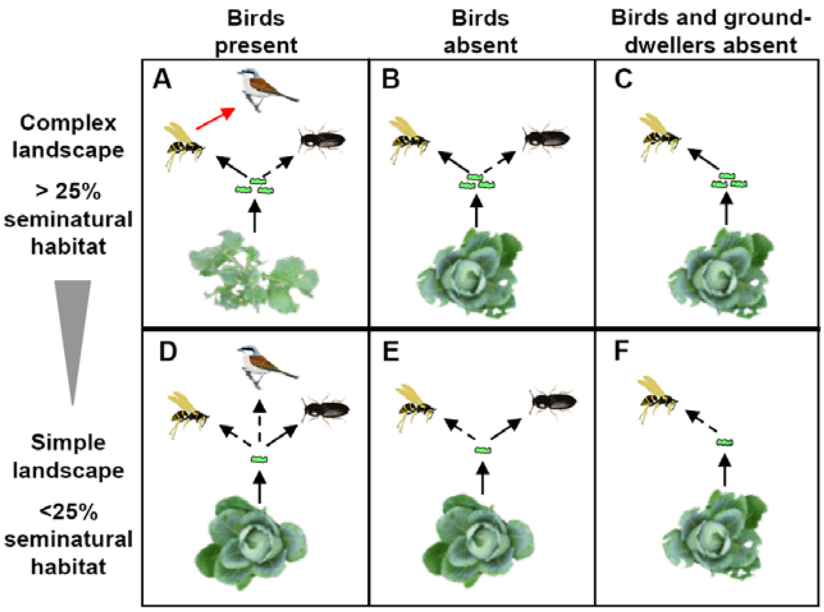

Figure 2.5. Summary of landscape effects on trophic interactions between natural enemies and their consequences for plant herbivory rates. a-c) Damage in complex landscapes (> 25% seminatural habitat) where herbivore pressure is strong (Figures 2.2, 2.3 B). d-f) Damage in simple landscapes where herbivore pressure is low. In complex landscapes, flying insects counterbalance herbivore pressure only when birds are absent (b-c); the relative contribution of ground-dwellers to control is low. In simple landscapes, mainly ground-dwellers counterbalance herbivore pressure (e-f); results also suggest a direct contribution to pest control by birds (d). Arrows show the direction of energy flows between trophic levels and guilds. Dashed arrows indicate low relative guild contribution compared to full arrows at the same trophic level. A red arrow between birds and flying insects indicates an antagonistic interaction by intraguild predation, which leads to high herbivory levels in complex landscapes. Degrees of herbivore damage on plants (strong, intermediate, low) are symbolized by different levels of leaf consumption. As overall herbivore pressure is low in simple landscapes, low pest control by flying insects (f) results in intermediate damage, similar to that in complex landscapes where the contribution of flying insects is high (c; Figure 2.3).

have a strongly disruptive character for pest control, omnivorous intraguild predation by birds on predatory wasps may be a relevant mechanism in this study (Polis et al., 1989; Straub et al., 2008) (Figure S2.3). However, detailed processes remain to be investigated at the level of species and population dynamics. Increasing intensity of intraguild predation in complex landscapes may be related to generally higher bird densities (Harvey et al., 2006), but also to higher densities of intraguild prey (Bianchi et al., 2006; Chaplin-Kramer et al., 2011), structural habitat differences (Janssen et al., 2007), and/or diet preferences. In contrast to expectations (Janssen et al., 2007), higher availability of complex habitats did not reduce intraguild predation in this study. Landscape complexity may indeed promote the co-occurrence of different natural enemies and thereby the probability of intraguild predation. Further, habitat configuration in complex landscapes may facilitate spillover of top predators from seminatural habitats into neighbouring crop fields (Bianchi et al., 2006), where the success of intraguild predation is high. Additionally, birds may optimize their foraging success by preying on flying insects in complex landscapes, but revert opportunistically to herbivore predation when flying insect abundance is low (Mooney et al., 2010).

Overall, these results are in line with the idea that complex landscapes may benefit generalist, fourth trophic level enemies, more than specialist third trophic level enemies (Rand et al., 2012), and shows for the first time that this can lead to a dampening of biological control. Previous work has shown that vertebrate predators can have net positive effects on plant productivity by reducing herbivorous arthropods, even as they also reduce intermediate arthropod predators (Mooney et al., 2010; Mäntylä et al., 2011). However, most of these studies were performed in forests, agroforests or plantations where spatial structures are presumably much less distinct than in mosaic agricultural landscapes dominated by annual crops. The present data confirm these results in simple, structurally homogeneous landscapes, but not in complex, structurally heterogeneous landscapes, where contiguity of very distinct habitats may create entirely different conditions for intraguild predation. However, despite its importance (Fahrig et al., 2011), no previous study of the effects of vertebrate predators on pest control has taken into account the landscape context in a replicated design (Mooney et al., 2010; Mäntylä et al., 2011).

Importantly, measures of crop damage and yield used in this study reflect the extent of effective crop protection by biological pest control until harvest (Thies and Tscharntke, 1999; Chaplin-Kramer et al., 2011). They are thus direct estimates of actual service provision for farmers, but have been rarely considered in studies at the landscape scale (Bianchi et al., 2006; Chaplin-Kramer et al., 2011), potentially because of the difficulty to measure effects of trophic cascades on plants under field conditions (Finke and Denno, 2004). In this study, negative natural enemy interactions in complex landscapes resulted in a trophic cascade harmful to plants and beneficial to herbivores (Finke and Denno, 2004; Duffy et al., 2007), which led to significant differences in crop damage and to corresponding effects on yield. Thus landscape-dependent mechanisms of pest suppression at higher trophic levels had landscape-wide consequences for services at the crop level (Knight et al., 2005), which were less significant but present at the level of yields.

In contrast to expectations, higher enemy functional diversity was not associated with better service provision in all landscapes (Finke and Denno, 2004; Tylianakis et al., 2007). Rather, effects of enemy functional diversity were positive in simple landscapes, but negative in complex landscapes. Unfortunately, no comparable study is currently available assessing the landscape-scale effects of more than two levels of functional diversity (Thies et al., 2005; Gardiner et al., 2009; Thies et al., 2011; Winqvist et al., 2011; Rand et al., 2012). Further research is thus needed to assess the general relevance of natural enemy interactions, which hold the potential to explain previously observed variation in landscape-scale responses of pest control services (Thies et al., 2005; Thies et al., 2011).

Research on the shifts in trophic interactions across landscapes can thus reveal the mechanisms behind observed patterns of ecosystem functioning and service provision. Precise mechanisms may include shifts in functional diversity, trophic structure and density-dependent changes in foraging strategies of local communities (Luck and Daily, 2003). Knowledge of these mechanisms is key to adequately formulating conservation and sustainable management schemes (Daily et al., 2009), because they increase the predictability of these schemes in real-world landscapes (Loreau et al., 2003; Carpenter et al., 2009). This study reveals the existence of contrasting interactions between natural enemies across landscapes, which constrained ecosystem service provision and reduced yields. It shows that trophic interactions are landscape-dependent, and that resulting ecosystem services are not deducible from patterns of species diversity only.

In conclusion, our study shows that simple solutions for biological pest control may not be available. Future management schemes need to take into account not only local habitat requirements, but also landscape composition and configuration, in order to reduce negative intraguild interactions and improve biological pest control. Landscape complexity may be beneficial to many ecosystem services, but can disserve others with far-reaching consequences. Knowing and deliberately balancing the tradeoffs at landscape scales between aims of species conservation, multiple ecosystem service provision and societal concerns is critical for the future of sustainability efforts and the ecological intensification of agriculture, and implies a deeper understanding of the underlying mechanisms.

2.4. Methods

Study region, landscapes and sites. Experimental plots were installed between July and September 2010 in 18 fields of a 55 km² agricultural landscape in Haean, South Korea (long. 128°5’ to 128°11’E, lat. 38°13’ to 38°20’N; Figure S2.1). This region is part of a 61.8 km² hydrological catchment located at the head of the Soyang Lake watershed, a major source of drinking water and energy for the northern half of South Korea (Park et al., 2010). Annual crop fields are generally small (mean±s.e.m 0.92±0.03 ha) and separated by seminatural margins. Compositional and configurational landscape heterogeneity (Fahrig et al., 2011) are high. Of the 18 study plots, 16 were located inside the catchment (Figure S2.1) and two were 20 km to the south, in an area with similar land use and climate. Thirteen of the plots were surrounded by organic fields and five by conventional ones, with variable crop composition. Fields were separated by at least 600 m, except the two outer fields distant by 210 m. They followed a gradient in landscape complexity ranging from 5.7% to 59.6% seminatural habitat in a 300 m radius around fields. ArcGIS 9.3 and R Statistical Software 2.13.1 (R Development Core Team, 2011) were used for landscape analyses of compiled Landsat imagery, regional land use maps and extensive ground-truthing in 2009 and 2010. Land cover class “seminatural” included seminatural field margins, intermediate regrowth and shrubby areas, forest edges, and 1-2 year old fallows. Undisturbed large forest areas and patches represent a specific, homogeneous habitat type and were thus considered as a separate land cover class (Fahrig et al., 2011). Pearson´s r correlations between main land cover classes and Shannon´s habitat diversity index are shown in Table S2.3.

Exclusion experiment. Experimental plots consisted of a 20 m² rectangle in a corner of each field, separated from the surrounding crop by 1.5 m high plastic mesh fences and a 2 m wide uncultivated buffer zone. Each plot bordered on seminatural edge habitats of similar structure and composition. They were planted between July 7th and 14th with seedlings of cabbage *Brassica oleracea* var. *capitata* at standard planting distances. After an initial 20 days, seven rows of four cabbages were randomly marked in each plot and all herbivores on these cabbages were removed. Initial herbivory rate (missing leaf area*100 / total leaf area of whole cabbages) was measured using a standardized metal grid (Kalka et al., 2008). Six exclusion treatments were installed on all plots, each around four cabbages (Figure S2.1). A seventh treatment excluding both herbivores and natural enemies controlled for differences in abiotic soil conditions (Figure S2.2). Ecofriendly pesticide was applied initially in this treatment only, and no other control agents were applied either in the plots or within the buffer zone between plots and field crops. After a 60-day growth period, treated plants were again measured for herbivory rate, then harvested and weighed for fresh biomass (total n = 432).

Treatments. Exclusion treatments consisted of 50*150*100 cm cages (Figure S2.1). Based on previous sampling, they were designed to exclude combinations of three main guilds of natural enemies: flying insects *F* (syrphid flies, parasitoid, predatory wasps); ground-dwellers *G* (carabid, staphylinid beetles, spiders); birds and other vertebrates larger than 1.5 cm *B* (Kalka et al., 2008). Cages were constructed using a) chicken wire with 1.5 cm mesh size (exclusion of birds and other vertebrates), b) polyester mesh with 0.8 mm mesh size (exclusion of all guilds), c) 3 mm thick clear plastic sheets, reaching up 25 cm on all sides and coated with a 10 cm wide continuous band of insect glue (exclusion of ground-dwellers). Microclimatic differences between treatments did not impact average biomass (Supplementary Methods). In treatments excluding ground-dwellers, cage sides were dug 20 cm into the ground and two live pitfall traps were maintained for the duration of the experiment. After initial capture of the ground-dwellers already present in the cages (day 2-3), pitfall traps remained empty throughout. An opening at the top of the cages, kept shut for the duration of the experiment, was used to access treated plants.

Arthropod standardization. Colonization of crop plants by pest arthropods is naturally very patchy, and this may lead to strong differences in damage and yield between neighbouring plants. In addition, natural enemy exclosures could also act as barriers for colonization by the dominant herbivores, here mainly the small and large whites *Pieris rapae* and *P. brassicae* and the cabbage looper *Trichoplusia ni*. In order to ensure that the differences between treatments were not concealed by random variation in colonization between plants, or biased by potential cage-induced differences in oviposition, initial pest densities were standardized between exclosures by carefully depositing the same number of larvae on all treated plants of a given plot (Figure S2.1). This procedure was necessary in order to allow subsequent comparison of the strength of pest control between treatments. It did not affect behaviour or health of the larvae. The number and instars of larvae to be deposited on plants of a given plot were determined using average density and larval stages found in the open treatment of the same plot. They were collected from plants in the surrounding field. Equilibration of pest densities was repeated after each round of arthropod monitoring in order to ensure that pest pressure was comparable between treatments for the duration of the experiment (see also Supplementary Methods; Figure S2.5).

Arthropod monitoring. Arthropods were monitored in each plot at three occasions throughout the growth period by carefully inspecting the leaves of all treated plants. Each monitoring round took place 10 days after equilibrating initial pest densities (Figure S2.5). Thus all rounds measured the same duration of exposure to pest control (10 days). Individual larval instars and oviposition were referenced in order to ensure that displaced individuals remained inside exclosures, and that densities inside exclosures continued to reflect approximate colonization rates (Supplementary Methods). Results are restricted here to densities of leaf-chewing Lepidoptera (responsible for herbivory); other pests included sap-sucking cabbage aphids *Brevicoryne brassicae* (Linné) and green peach aphids *Myzus persicae* (Sulzer). Pest densities are given as the total number of larvae of Lepidoptera in each exclusion cage. These include larvae of *P. rapae*, *P. brassicae* and *T. ni*, all native to the region. In one plot (19.2% seminatural habitat at the 300 m scale), only two monitoring rounds could be performed. Thus replicates are 6 treatments * 17 plots * 3 rounds + 6 treatments * 2 rounds (total n = 318).

Statistical analyses. Pest density (n = 318), herbivory rate and biomass (n=432) were analyzed using mixed effects models in R Statistical Software 2.13.1 (R Development Core Team, 2011). Herbivory was logit-transformed (Warton and Hui, 2011) and variance functions were used to model heteroscedasticity (Zuur et al., 2009) in a linear mixed effects model with package nlme. Pest density was modelled with a negative binomial 1 error distribution for count data with overdispersion, and biomass with a Gamma distribution for positive continuous data, using generalized mixed effects models (glmm) in package glmmADMB. Explanatory variables were treatment (6 levels of natural enemy exclusion), % seminatural habitat, two independent covariates (crop and management type of the nearest surrounding field; Supplementary Methods), and associated 2-way and 3-way interactions. Random effects were exclusion treatment nested within plot for herbivory and biomass of individual plants. Pest density (the total number of larvae per treatment) included the crossed random effects plot and sampling round. Analyses were performed at all spatial scales (with 100 m intervals) between 100 m and 1000 m around fields. The most predictive scale (300 m) was determined by Akaike Information Criterion (AIC) comparison of the full models at all scales (ΔAIC>4) and used for final model selection. Minimum adequate models were selected by maximum likelihood ratio tests comparing models with nested fixed effects (Zuur et al., 2009). The variable % seminatural habitat and the interaction between treatment and % seminatural habitat were selected in all cases (Table 2.1). These effects were maintained at scales from 100 to 700 m around fields. In addition, if landscape complexity was calculated as Shannon´s index of habitat diversity, patterns were identical and significant for herbivory at scales from 100 to 900 m around fields (Table S2.2, Figure S2.4). However, neither % forest nor a combined metric (% forest + % seminatural habitat) had any effect on response variables. Model residuals were inspected for spatial autocorrelation and violation of assumptions of normality and homoscedasticity. Multiple comparisons were performed using a manually defined contrast matrix with p-values adjusted for the False Discovery Rate (Benjamini and Yekutieli, 2001). In order to favour interpretation, predicted herbivory values were backtransformed taking into account estimation uncertainty (Jørgensen and Pedersen, 1998) (Supplementary Methods) and used to estimate the degree of actual pest control occurring in the treatments, as the difference between herbivory in the presence of enemies and herbivory in their absence.

2.5. Acknowledgments

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2.7. Supplementary Methods

Arthropods. At each standardization (Figure S2.5), on average 1 to 2 larvae were added or removed per plant to account for patchy differences in colonization. Standardizations are equivalent to simulating homogeneous (the same for all plants), instead of heterogeneous, pest colonization rates, and thus render measures of pest control comparable between treatments. Actual rates of pest control are unchanged and are maintained throughout the experiment. While this procedure limits the effects of patchy colonization, it remains a discrete compensation for a process that is continuous throughout the season. Any bias in colonization between the treatments, occurring in the period between standardizations (Figure S2.5), would lead to an underestimation of herbivory in controls excluding enemies. Thus actual rates of pest control (the difference between effects with and without enemies) could potentially be higher, but not lower, than suggested by our results.

At each standardization, mean pest densities are homogenized between plants, but remain constant at the plot level. Thus measures of pest density, damage and biomass of open, treated plants remain comparable to those of non-treated plants in the same plots. Independently of standardizations, effects on these plants are thus comparable to the actual effects encountered by farmers when pesticides are not applied.

Covariates. Two covariates were included in all models to account for differences between selected fields. Covariates were a) the crop type of the nearest surrounding field (Brassicaceae/non-Brassicaceae), and b) the management intensity of the nearest surrounding field (organic/conventional). Covariates did not correlate significantly either with % seminatural habitat (Pearson´s r=0.01, p=0.95 and r=0.3, p=0.2, for crop and management respectively) or with each other (r=0.12, p=0.6). Crop type of the nearest surrounding field had no significant effect and was discarded from all models. Management intensity was retained as a significant independent factor for herbivory and biomass responses, but not for pest density (Figure 2.2, S2.2).

Microclimate controls. Fine mesh with <1 mm diameter efficiently excludes flying insect enemies including parasitoids (treatments -G-F-B and -F-B). However, it can lead to microclimatic and light differences between treatments. These were controlled by placing two Thermochron iButton® temperature loggers (Fuchs Elektronik, serial # DS1921G-F5#), protected from rain, wind and direct sunlight, at plant height in each plot, one in the open, the other inside a fine mesh treatment. Temperatures were 0.56±0.1°C higher inside fine mesh treatments than outside (mean±s.e.m.; t=5.5, df = 17, p<0.001). Air humidity was measured at random hours on five sunny and five rainy days, using one Exoterra® hygrometer inside and one outside fine mesh treatments. It was not significantly different in either sunny or rainy conditions, inside and outside treatments (t=1.4, p=0.3 and t=-0.4, p=0.7, respectively). Mesh transparency, measured at five occasions using a LI-190 Quantum Sensor (Li-Cor®), was 83±0.9% (mean±s.e.m.). In order to test whether fine mesh exclosures led to biomass differences between plants independently of herbivore pressure, we used a subset of plants from open treatments where total herbivory was <1% (n = 9), and compared them to exclosed plants of the same plots with similarly low herbivory (additional treatment excluding herbivores and enemies with herbivory always <1%; n=22; Methods). No significant differences in biomass were found between open and exclosed plants with similarly low herbivory rates (n = 31 grouped in 6 plots, F = 0.19, p = 0.68; linear mixed effects model with treatment within plot as random variables).

Backtransformation function. A) Code of the generic backtransformation function used in R Statistical Software (33), based on model estimates (mean) and their standard deviations (sd). This function takes into account the variation associated with each model estimate by integrating their errors within a random sample of estimates. B) Backtransformation of logit-transformed herbivory, using the inverse-logit function plogis() (R package: stats). Errors are integrated from –Inf to +Inf.

A

```
inv.generic <- function(mean, sd, backfun = function(x) x, lower.lim = -Inf, upper.lim = Inf ) {
data <- cbind(mean, sd)
foo <- function(x, mean, sd) {
exp(log(backfun(x)) + dnorm(x, mean, sd, log=TRUE))
}
apply(data, 1, function(x) integrate(foo, lower=lower.lim, upper=upper.lim, mean=x[1], sd=x[2])$value)
}
```

B

```
inv.generic(mean, sd, backfun = function(x) plogis(x))
```

2.8. Supplementary Tables

Table S 2.1. Multiple comparisons between enemy contributions to A) pest density reduction and B) biomass increase, across the gradient in landscape complexity.

Treatments	Enemy contributions	Value	SE	z	p	p (adjusted)
A. Pest density						
Slope differences						
-G-B vs. -F-B	🐝 **vs.** 🪲	**-0.044**	**0.019**	**-2.619**	**0.009 ****	**0.035 ***
-G-B vs. -G	🐝 **vs.** 🐦🐝	**0.037**	**0.019**	**2.863**	**0.004 ****	**0.031 ***
-G-B vs. -B	🐝 vs. 🪲🐝	0.009	0.022	0.447	0.655	0.707
-G-B vs. O	🐝 **vs.** 🐦🪲🐝	**-0.040**	**0.014**	**-3.382**	**0.001 ****	**0.012 ***
-F-B vs. -B	🪲 vs. 🪲🐝	-0.036	0.021	-2.097	0.036 *	0.115
-F-B vs. O	🪲 vs. 🐦🪲🐝	0.004	0.012	-0.437	0.662	0.707
-G vs. O	🐦🐝 vs. 🐦🪲🐝	-0.003	0.012	-0.494	0.621	0.707
-B vs. O	🪲🐝 **vs.** 🐦🪲🐝	**-0.032**	**0.016**	**-2.758**	**0.006 ****	**0.031 ***
Intercept differences						
-G-B vs. -F-B	🐝 vs. 🪲	1.043	0.666	1.828	0.068 .	0.180
-G-B vs. -G	🐝 vs. 🐦🐝	-0.418	0.644	-0.947	0.344	0.596
-G-B vs. -B	🐝 vs. 🪲🐝	-0.602	0.700	-0.926	0.354	0.596
-G-B vs. O	🐝 vs. 🐦🪲🐝	0.609	0.452	1.743	0.081 .	0.186
-F-B vs. -B	🪲 vs. 🪲🐝	0.441	0.693	0.892	0.373	0.596
-F-B vs. O	🪲 vs. 🐦🪲🐝	-0.434	0.445	-0.264	0.792	0.792
-G vs. O	🐦🐝 vs. 🐦🪲🐝	0.191	0.414	0.794	0.427	0.621
-B vs. O	🪲🐝 vs. 🐦🪲🐝	0.007	0.510	0.709	0.478	0.638
B. Biomass						
Slope differences						
-G-B vs. -F-B	🐝 vs. 🪲	0.031	0.015	2.005	0.045 *	0.113
-G-B vs. -G	🐝 vs. 🐦🐝	-0.031	0.015	-2.040	0.041 *	0.113
-G-B vs. -B	🐝 vs. 🪲🐝	-0.031	0.015	-2.010	0.044 *	0.113
-G-B vs. O	🐝 vs. 🐦🪲🐝	0.034	0.015	2.226	0.026 *	0.113
-F-B vs. -B	🪲 vs. 🪲🐝	0.000	0.015	-0.004	0.997	0.997
-F-B vs. O	🪲 vs. 🐦🪲🐝	0.003	0.015	0.220	0.826	0.909
-G vs. O	🐦🐝 vs. 🐦🪲🐝	0.003	0.015	0.186	0.853	0.909
-B vs. O	🪲🐝 vs. 🐦🪲🐝	0.003	0.015	0.216	0.829	0.909
Intercept differences						
-G-B vs. -F-B	🐝 vs. 🪲	-0.817	0.485	-1.685	0.092 .	0.184
-G-B vs. -G	🐝 vs. 🐦🐝	0.953	0.485	1.966	0.049 *	0.113
-G-B vs. -B	🐝 vs. 🪲🐝	1.090	0.485	2.249	0.025 *	0.113
-G-B vs. O	🐝 vs. 🐦🪲🐝	-1.344	0.485	-2.772	0.006 **	0.089 .
-F-B vs. -B	🪲 vs. 🪲🐝	0.274	0.485	0.565	0.572	0.801
-F-B vs. O	🪲 vs. 🐦🪲🐝	-0.527	0.485	-1.088	0.277	0.492
-G vs. O	🐦🐝 vs. 🐦🪲🐝	-0.391	0.485	-0.807	0.420	0.672
-B vs. O	🪲🐝 vs. 🐦🪲🐝	-0.254	0.485	-0.523	0.601	0.801

Tests are based on the model contrast matrices of pest density and biomass (adjusted p-values: Benjamini-Hochberg method). *-G-B*: exclusion of ground-dwellers and birds; *-F-B*: exclusion of flying insects and birds; *-B*: exclusion of birds; *-G*: exclusion of ground-dwellers; *O*: no exclusion. Statistically significant differences between enemy guilds are indicated in bold (significance codes ‘***’ p<0.001, ‘**’ p<0.01, ‘*’ p<0.05, ‘.’ p<0.1).

Table S 2.2. Results of mixed effects models using Shannon´s habitat diversity index (SHDI) as landscape complexity metric instead of % seminatural habitat (Table 2.1). Response variables are pest larval density, herbivory and biomass (n = 318 and 432 in 18 plots). Spatial scale is 300 m around fields.

Explanatory variables (before selection)	nDF	dDF	Test statistic	p-value	
Pest larval density			Deviance		
Treatment	5	-	5.34	0.376	
SHDI	1	-	6.1	0.014	*
Treatment X SHDI	5	-	11.23	0.047	*
Herbivory (%)			F		
Treatment	5	80	14.83	<.0001	***
SHDI	1	15	0.95	0.346	
Management intensity	1	15	3.02	0.103	
Treatment X SHDI	5	80	2.9	0.019	*
Biomass (g)			Deviance		
Treatment	5	-	7.22	0.205	
SHDI	1	-	0.06	0.807	
Management intensity	1	-	6.52	0.011	*
Treatment X SHDI	5	-	8.02	0.155	

See Methods and Table 1 for statistics. nDF: numerator degrees of freedom, dDF: denominator degrees of freedom (significance codes ‘***’ p<0.001, ‘**’ p<0.01, ‘*’ p<0.05).

Table S 2.3. Pearson´s r correlations between the proportions of main land cover classes and Shannon´s index of habitat diversity (SHDI), calculated at the 300 m scale around fields.

Metrics	Pearson´s r
% Forest vs. % Seminatural habitat	-0.53
% Arable vs. % Seminatural habitat	0.28†
% Forest vs. % Arable	-0.92
SHDI vs. % Forest	-0.55
SHDI vs. % Seminatural habitat	0.41
SHDI vs. % Arable	0.47

† % Seminatural habitat is highest at intermediate amounts of arable land.

2.9. Supplementary Figures

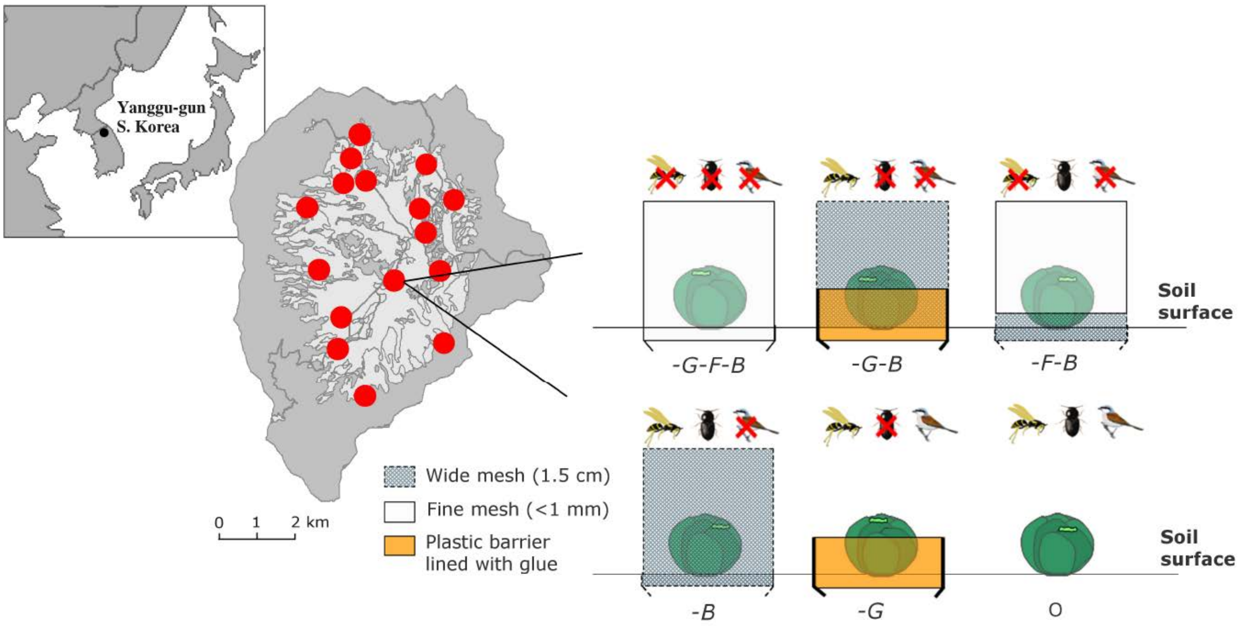

Figure S 2.1. Study design showing the location of 16 plots (red dots) in the Haean catchment, Yanggu-gun, South Korea (2 sites outside the catchment are not shown), and natural enemy exclusion treatments in each plot. The northern edge of the mountain-ringed catchment is ca. 500 m from the border to North Korea. The structure of natural enemy exclosures is shown in a lateral view (cage sides are dug 10-20 cm into the ground). Each exclosure contains 4 plants (n = 432). Treatments are: *-G-B-F* (control; exclusion of all enemies), *-G-B* (exclusion of ground-dwellers and birds, but not flying insects), *-F-B* (exclusion of flying insects and birds), *-B* (exclusion of birds), *-G* (exclusion of ground-dwellers), *O* (open treatment, no exclusion).

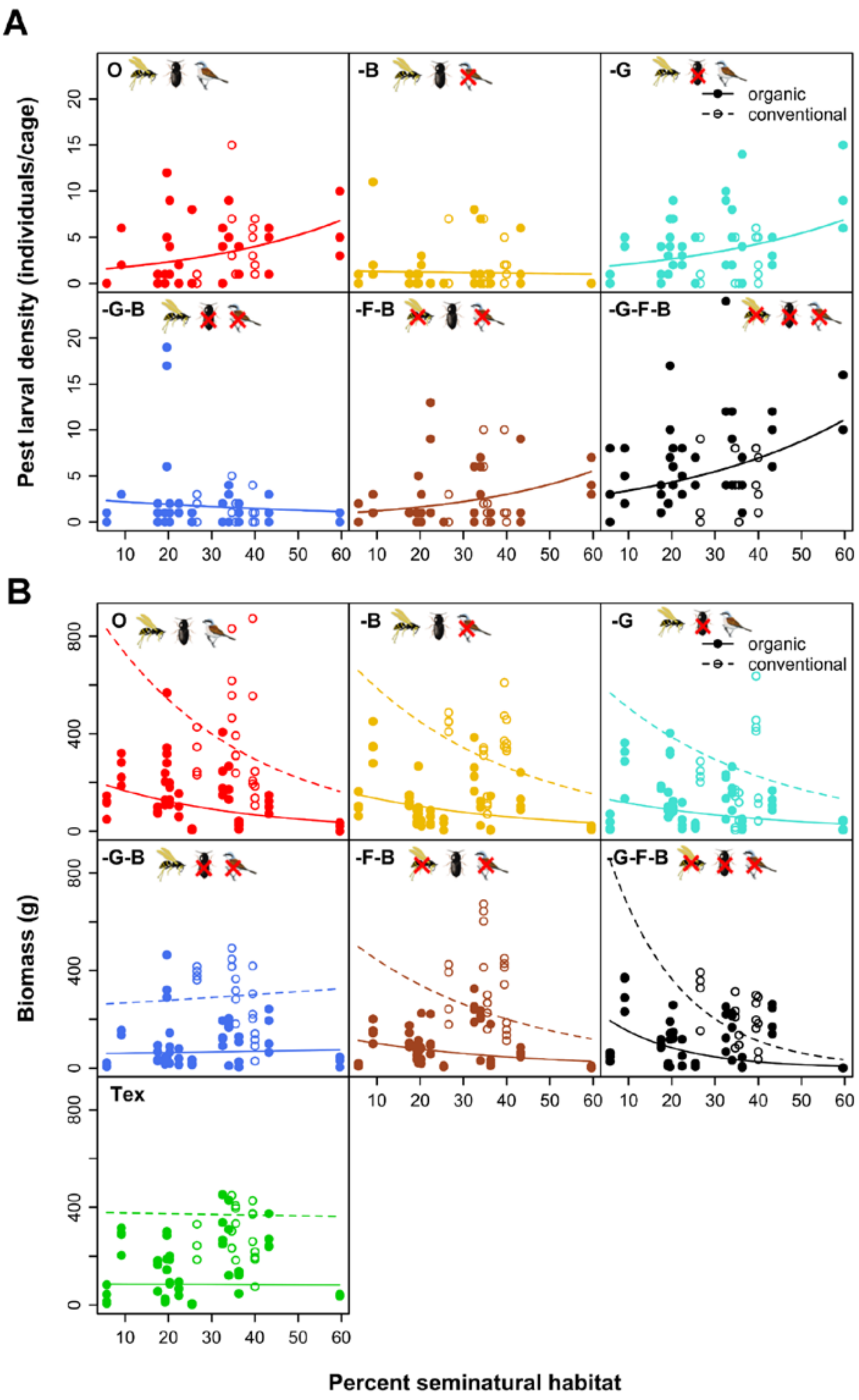

Figure S 2.2. Effects of landscape complexity and management on A) pest larval density and B) fresh crop biomass (g) in six natural enemy exclusion treatments and total exclusion control. Pest densities are measured per exclusion cage in each of three sampling rounds (n = 318). Biomass is measured per individual cabbage plant (4 plants per exclosure; n = 432). Regression lines represent predicted model results. Interactions between landscape complexity and exclusion treatment were significant (Table 2.1; multiple comparisons, Table S2.1). Full points and solid lines: organic management of the nearest surrounding field (13 plots), open points and dashed lines: conventional management of the nearest surrounding field (5 plots). O: open treatment without exclusion; -G: exclusion of ground-dwellers; -B: exclusion of birds; -F-B: exclusion of flying insects and birds; -G-B: exclusion of ground-dwellers and birds, but not flying insects; -G-F-B: control excluding all enemies but including herbivores; Tex: total exclusion of enemies and herbivores (abiotic control).

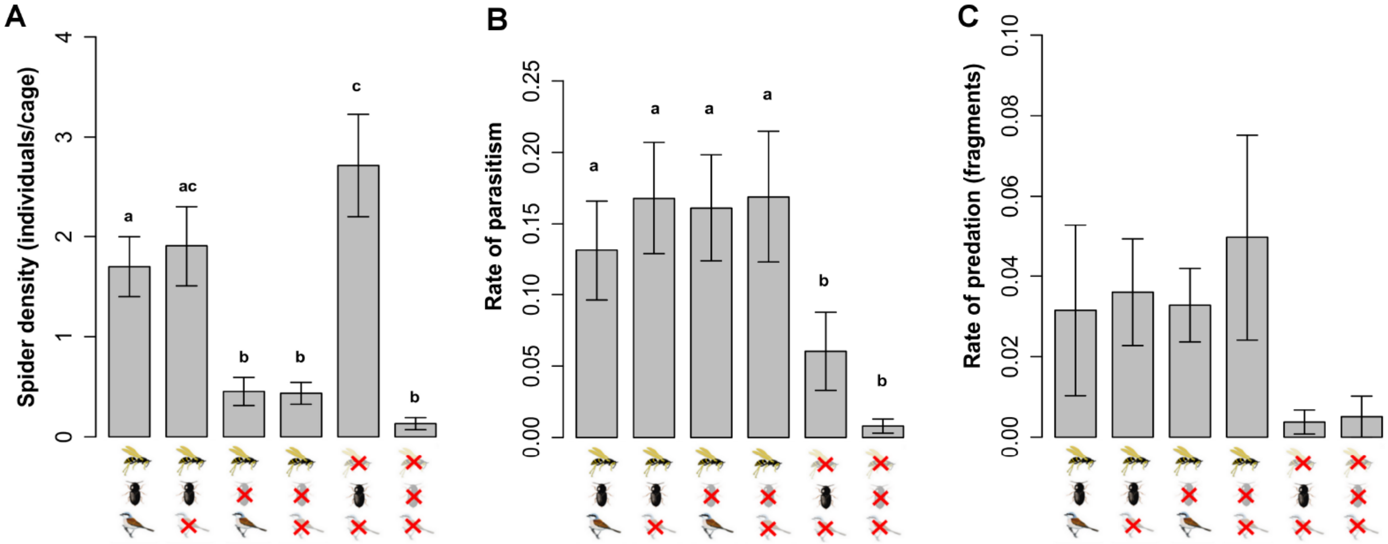

Figure S 2.3. Effectiveness of exclosures and differences in natural enemy activity in six exclusion treatments. Although enemy abundances could not be measured for all guilds, the following data are available. A) Mean ± s.e.m. spider density in six natural enemy exclusion treatments. Spider densities were only affected by treatment differences and not by landscape complexity (negative binomial 1 glmm, $p<0.001$). Densities were low in all ground-dweller exclusion treatments. They were not affected by the presence of birds, but were slightly lower in the presence of flying insects (possibly due to spider-hunting wasps). B) Mean ± s.e.m. rates of parasitism of lepidopteran larvae by parasitoids in all treatments ($N_{parasitized}$ / N_{total}; binomial glmm, $p <0.001$). Parasitism was reduced in treatments excluding flying insects, but showed no differences between treatments allowing their access. C) Mean ± s.e.m. rates of predation, calculated based on the number of remaining “fragments” of lepidopteran pest larvae ($N_{fragments}$ / N_{total}; binomial glmm, $p = 0.03$). These fragments are characteristic of predation by predatory wasps on large instars of pest larvae, and are thus likely to be linked to this guild of predators. Their presence in all treatments not excluding flying insects indicates wasp activity in the plots. Different letters show significant differences between treatments (adjusted p-values). Detailed legend description is provided in Figure 2.1.

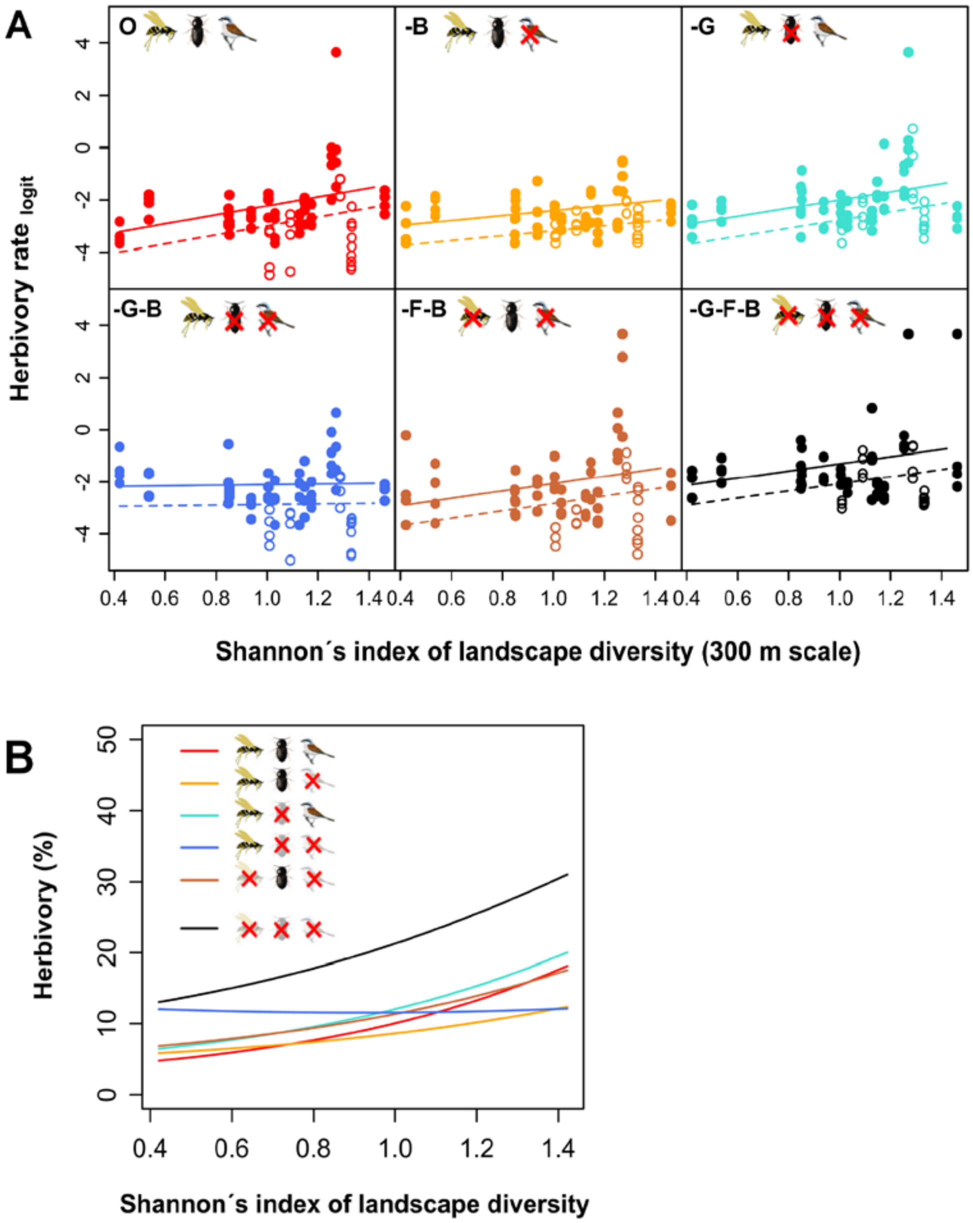

Figure S 2.4. Effects of habitat diversity on herbivory in six natural enemy exclusion treatments, using Shannon´s habitat diversity index (SHDI) as a metric instead of % seminatural habitat. Spatial scale shown is 300 m around fields. A) Logit-transformed herbivory per treatment across the landscape gradient. B) Back-transformed herbivory in all treatments across the landscape gradient. Lines show (backtransformed) predicted values of linear mixed effects models. See detailed legend description in Figure 2.1. For corresponding statistics see Table S2.2.

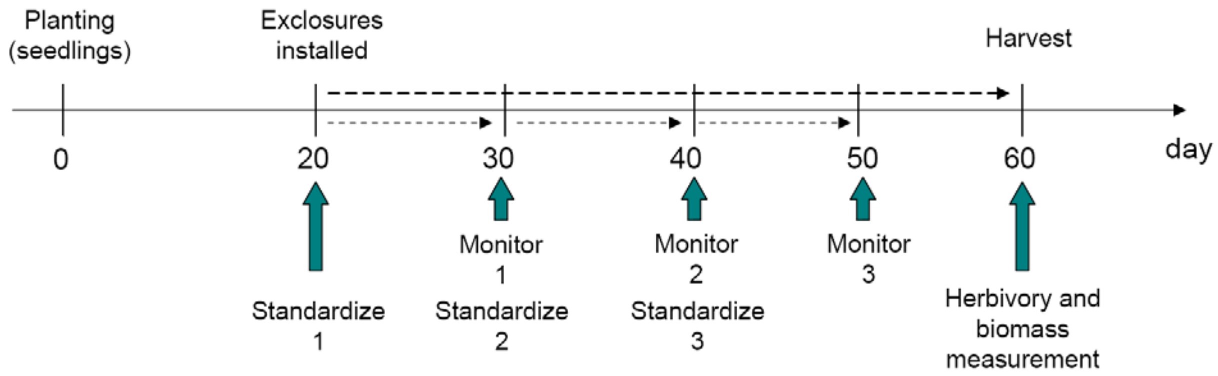

Figure S 2.5. Temporal sequence of the study. At the start of the experiment (day 20 after planting), initial densities of pest larvae are equilibrated between all treatments (Standardize 1; Methods and Supplementary Methods). After 10 days of exposure to pest control, larvae are monitored (Monitor 1), then equilibrated once more for the next round of pest control (Standardize 2). This is repeated at 10 day intervals. The large dashed arrow shows total duration of the experiment; small dashed arrows show the duration of pest control exposure with equal initial densities (10 days).

Chapter 3

3. Pest control of aphids depends on landscape complexity and natural enemy interactions

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Abstract

1. Pest control of aphids is a major concern in agricultural crops worldwide, and reducing pesticide use in favor of control by natural enemies is an essential component of the ecological intensification of agriculture. Although the natural enemies of pests are known to be influenced by the complexity of agricultural landscapes, few studies have measured the actual degree of pest control occurring across gradients in landscape complexity, and the precise mechanisms underlying landscape effects on pest control are largely unknown.

2. Here, we use multiple natural-enemy exclosures replicated across a gradient in landscape complexity to investigate 1) the strength of natural pest control across landscapes, measured as the difference between pest pressure in the presence and in the absence of natural enemies; 2) the differential contributions of natural enemy guilds to pest control, and the nature of their interactions across landscapes.

3. We show that natural pest control of aphids increased up to six-fold from simple to complex landscapes. Aphid densities in the absence of pest control were higher in complex than simple landscapes, but were reduced by natural enemies to similar densities across landscapes.

4. Importantly, the interactions and relative contribution to control of enemy guilds were landscape-dependent. Particularly in complex landscapes, total pest control was formed by the combined contribution of flying insect enemies and ground-dwelling predators, but flying insects contributed two times more to control than ground-dwellers. Birds had little overall impact on aphid control. Despite evidence for intraguild predation of flying insects by ground-dwellers and birds, the overall effect of enemy guilds on aphid control was complementary.

6. *Synthesis and applications.* Predicting the effectiveness of pest control services at large spatial scales is critical to increase the success of ecological intensification schemes in agricultural landscapes, and hinges on our ability to disentangle the interaction mechanisms of pest control along gradients of landscape complexity. Our results suggest that, where aphids are the main pest of concern, largely complementary interactions between natural enemies drive a strongly positive effect of landscape complexity on natural pest control.

Keywords

Agroecosystem, biodiversity-ecosystem functioning, cabbage *Brassica oleracea* var. *capitata*, land use intensification, proportion of seminatural habitat, South Korea, trophic interactions.

3.1. Introduction

Pest control by natural enemies is an essential ecosystem service valued at $4.49 billion annually in the USA alone (Losey and Vaughan, 2006). In the context of increasing pressure to reduce harmful chemical inputs while maintaining or increasing current agricultural yields, the gradual replacement of conventional agricultural practices with natural pest control provided by functional ecosystems is a major hope for the future (Bommarco et al., 2013). However, current understanding of the flow and stability of pest control services in human-modified systems is limited, and constrains our ability to implement an ecological intensification of agriculture (Rusch et al., 2013).

The distribution and abundance of agricultural pests and their natural enemies are known to be influenced by the landscape context surrounding crop fields (Bianchi et al., 2006). In landscapes with high amounts of complex or seminatural habitats, enemies such as parasitoid wasps, predatory beetles, and insectivorous birds are frequently more abundant and species-rich than in simplified landscapes with large monocultures and little complex habitat. These effects vary according to the enemies considered and the spatial scale of observations (Chaplin-Kramer et al., 2011), and are strongest for enemies that depend on permanent habitat structures for nesting, overwintering and other food resources (Bianchi et al., 2006). In contrast, effects of landscape context on pest distributions are less well understood and appear highly variable between systems and years (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). As pest distributions are a reflection of landscape effects on the pests themselves, but also of their suppression by natural enemies in the same landscape over more than one season (Chaplin-Kramer and Kremen, 2012), estimating the effects of landscape context on pests and thus on pest suppression requires distinguishing their abundance in the presence of enemies, from what it would be without them. However, the direct effect of landscape context on the strength of pest suppression by natural enemies has only rarely been measured (Chaplin-Kramer et al., 2011) and may not show a direct relationship to the abundance and richness of natural enemies in the same landscapes (Letourneau et al., 2009).

Effects of natural enemies on pests can involve multiple interactions that prevent them from being deducible from the diversity of the natural enemy community (Martin et al., 2013). These interactions can be additive or synergistic, i.e. pest control by multiple enemies is as strong or stronger than the sum of each enemy's effect in isolation; neutral, i.e. pest control is similar whether enemies are combined or not; or antagonistic, i.e. negative interactions such as intraguild predation or behavioral interference lead to lower pest control when enemies are combined than in isolation (Letourneau et al., 2009). These effects are determined by a variety of possible mechanisms, including niche complementarity and functional redundancy in addition to intraguild predation (Straub et al., 2008; Tylianakis and Romo, 2010), and may also be affected by the complexity of local vegetation structures (Janssen et al., 2007). However, in terrestrial systems, interactions of species and functional groups have almost exclusively been investigated at small spatial and temporal scales that do not reflect the complexity of real-world landscapes (Duffy et al., 2007; but see Thies et al., 2011; Holland et al., 2012). Results of these local studies show highly unpredictable interactions across systems and organisms, and little consensus has been reached on the factors that determine interaction strength and direction in real-world ecosystems (Tylianakis and Romo, 2010). Thus, although pest control requires the presence of natural enemies in the system, its effectiveness can only be approximated by measures of enemy diversity if the direction of enemy interactions is known across all relevant spatial and temporal scales. Quantifying effective pest control across landscapes requires measuring the effects of the entire pool of enemies; predicting variations of these effects requires identifying the individual contributions of different enemies to pest control and the nature of their interactions across landscapes (Martin et al., 2013).

In this study, we use multiple natural enemy exclosures on pests of cabbage *Brassica oleracea* var. *capitata* in a replicated design across landscapes of an agricultural region of South Korea. We aim 1) to assess the strength of pest control by all natural enemies combined on aphid populations, across a gradient in landscape complexity; 2) to identify the separate contributions of each functional guild of natural enemies to pest control at the landscape scale and the nature of enemy interactions across landscapes. We hypothesize that interactions of the natural enemy pool may change with landscape complexity due to changing amounts of seminatural habitat as a refuge against intraguild predation (Janssen et al., 2007), contiguity of more distinct habitats intensifying spillover, and changing density ratios between pests, enemies, and among enemy functional guilds (Bianchi et al., 2006; Chaplin-Kramer et al., 2011); and that this has consequences for overall pest control strength (Martin et al., 2013). The main functional guilds of natural enemies distinguished here are birds and other vertebrates larger than 1.5 cm; flying insects including syrphid flies, parasitoid and predatory wasps; and ground-dwellers including spiders, carabid and staphylinid beetles.

3.2. Materials and Methods

Study site and experiment. This experiment was performed from July to September 2010 in the 55 km² agricultural region of Haean, South Korea (long. 128°5’ to 128°11’E, lat. 38°13’ to 38°20’N; Figure S3.1). In this region, annual and perennial crops are cultivated in fields <1ha separated by seminatural margins. Patches of deciduous forest and riparian corridors are distributed throughout, contributing to high landscape heterogeneity.

Eighteen fields were selected in this region (Martin et al., 2013), of which 13 were managed organically and five conventionally. Mean distance between fields was 7.6±0.7 km (mean ± SE) with a minimum distance of 630 m except two plots distant by 211 m. The field locations covered a gradient in landscape complexity from 6.3% to 43.3% seminatural habitat in a 700 m radius around fields, and bordered on seminatural margins of similar size and plant composition. Within each field, one 20 m² plot was separated from the surrounding crop and planted with cabbage *Brassica oleracea* var. *capitata*. No pesticides were applied on these plots. After an initial 20 days, six rows of four cabbages were randomly marked in each plot from which all herbivores were removed. Six natural enemy exclusion treatments were installed on these plants between day 20 and 21 and maintained until harvest after 60 days.

In order to initialize treatments of each plot at similar densities (Chaplin-Kramer and Kremen, 2012), the number of aphids per plant was standardized at the start of the experiment by placing on each treated cabbage the average number of aphids per plant found in the plot. As densities were low at the start of the season, aphids thus inoculated in each plot varied from 2 to 10 per plant. In plots where no aphids were present at the beginning of the experiment, a minimum of 2 aphids per plant was inoculated. Cabbage leaves infested with laboratory-reared cabbage aphids *Brevicoryne brassicae* (Linné) were transported to the field and fragments with the approximate number of aphids were deposited on treated cabbages. After one day, successful transfer of the desired number of aphids to treated plants was verified and any aphids in excess were removed.

Starting 10 days after initializing the treatments, arthropods were monitored at three occasions (10 day intervals) throughout the growth period, by carefully inspecting both sides of leaves and recording the number, species and life stage of arthropod herbivores, parasitoids and predators, mainly the larvae of syrphid flies. Sap-sucking species included cabbage aphids *Brevicoryne brassicae*, green peach aphids *Myzus persicae* (Sulzer) and low densities of the turnip aphid *Lipaphis erysimi* (Kaltenbach). Larvae of the leaf-chewing Lepidoptera *Pieris rapae*, *Pieris brassicae* (Linné) and *Trichoplusia ni* (Hübner) were present and their effects are described in a separate publication (Martin et al., 2013a). After 60 days, cabbage plants were harvested and weighed for fresh biomass. As one plot was monitored on two occasions only, the total number of observations is 17 plots × 6 treatments × 4 plants × 3 rounds + 1 plot × 6 treatments × 4 plants × 2 rounds = 1272.

Field exclusion treatments. Natural enemy exclusion treatments were cages designed to exclude combinations of three guilds of natural enemies: G - ground-dwellers (spiders, carabid and staphylinid beetles), F - flying insects (syrphid flies, parasitoid and predatory wasps), and B - birds and other vertebrates larger than 1.5 cm. Cages were 50*150*100 cm and covered one row of four cabbage plants. We used combinations of chicken wire (1.5 cm mesh size), fine polyester mesh (0.8 mm) and plastic barriers coated with insect glue to exclude either all enemies (treatment -G-F-B, “no enemy” control), birds and flying insects (-F-B), ground-dwellers and birds (-G-B), only ground-dwellers (-G), only birds (-B), or no enemies (O, open control; see (Martin et al., 2013) for more detailed treatment description). An additional treatment excluding both enemies and herbivores controlled for abiotic soil conditions between plots; ecofriendly pesticide was applied at the start of the experiment in this treatment only. Differences in soil conditions between plots had no effect on final cabbage biomass (Martin et al., 2013). At the start of the experiment, two live pitfall traps were installed in all treatments excluding ground-dwellers. After initial collection of the ground arthropods already present, pitfall traps remained empty throughout the experiment. This method was effective also for spider exclusion (Martin et al., 2013a). Microclimatic and light differences between treatments were tested in each plot and had no significant effect on plant growth between treatments (Martin et al., 2013a). As only 2.2% of aphids were winged (700 out of 31,503 counted individuals), the role of aphid dispersal appears to have been negligible (Thies et al., 2011).

Data analysis. Aphid density, population growth, parasitism rate (the ratio of parasitized to all aphids) and syrphid:aphid ratio (the ratio of syrphid larvae to all aphids) were analyzed using linear and generalized linear mixed models in R Statistical Software 2.13.1 (R Development Core Team, 2011). Aphid density (n = 1272) was square-root transformed and variance functions were used to model heteroscedasticity. Total aphid population growth was calculated as the log-ratio of aphid density in round 3 and aphid density in round 1 (20 days apart; n = 408; 17 plots). Both were analyzed using linear mixed models in package nlme (Pinheiro et al., 2013). Parasitism rate and syrphid:aphid ratios were modelled using a binomial response with logit link in package lme4 (Bates et al., 2013). An observation-level random effect was included in generalized linear models to account for overdispersion. All models included ‘exclusion treatment’ (6 levels of natural enemy exclusion) nested within ‘plot’ (18 plots, each in one landscape sector) as random effects, in order to account for spatial pseudoreplication within each plot and exclusion treatment. Explanatory variables included exclusion treatment, percent seminatural habitat in a radius around each plot, sampling round (1-3), management type of the surrounding field (organic / conventional), crop type of the surrounding field (Brassicaceae / non Brassicaceae), and 2-way and 3-way interactions. Management and crop type did not correlate significantly either with percent seminatural habitat (Pearson´s r = 0.3, p = 0.2 and r=0.01, p=0.95, respectively) or with each other (r=0.12, p=0.6).

In order to determine the most adequate spatial scales for analysis of each response variable, Akaike´s Information Criterion (AIC) was used to compare the full models at 100 m-intervals between 100 m and 1000 m around fields, the extent of scales tested being restricted by the small size of the sampling region. Lowest AIC values were selected at 700 m for aphid density and 1000 m for other variables, and results are shown for these most predictive scales. However, effects of landscape and landscape:treatment interactions were also selected with similar effects in model confidence sets (see below) at all tested scales, with a lowest probability of 30% at the 500 m scale (Table S3.1).

Model selection was performed for each response variable by assembling a 95% confidence set of models (cumulated sum of AIC weights ≤ 95%) from the set of all possible models, using sequential AIC testing with the function “dredge” in R package MuMIn (Barton, 2012). Model averaging was performed on this set and weights were calculated for each explanatory variable as the sum of the AIC weights of each model it occurs in. Weights of each explanatory variable can thus be interpreted as the probability of its presence, or importance, within the global averaged model (Burnham et al., 2011). Predicted values were obtained from averaged model coefficients. Tukey multiple comparisons of means were performed on models without interactions, and slope comparisons of models with interactions were performed using manually defined contrast matrices. P-values of multiple comparisons were adjusted for the False Discovery Rate. Models were checked graphically for violation of assumptions of normality and homoscedasticity. Spline correlograms confirmed that any spatial autocorrelation present in the raw data was accounted for by inclusion of the model random effects (Zuur et al., 2009).

In order to estimate the importance of parasitism and syrphid predation for aphid suppression and biomass increase, we used a separate set of linear regressions relating aphid population growth and final crop biomass to enemy:aphid ratios and enemy densities.

Mean percent aphid reduction across rounds compared to controls without enemies was calculated from model predicted values as $(N_{treatment}-N_{control})/N_{control}$ with N = mean aphid density across landscapes.

3.3. Results

Effects of enemy exclusion and landscape context on aphid densities

On average, aphid densities were 77% (range 62-92%) lower in the presence of all natural enemies than in their absence (Figure 3.1; Table 3.1). This effect was maintained across sampling rounds, with densities in treatments accessible to natural enemies reaching near-zero values at the end of the season (0.65±0.28 aphids/plant), while densities remained higher in treatments excluding all enemies (43.28±12.98 aphids/plant). Separate enemy guilds reduced aphid densities to lower values than in their absence, with on average 45% (18-69%) and 64% (47-78%) reduction by ground-dwellers and flying insect enemies, respectively. Direct effects of vertebrate predators (birds) are not measurable in isolation from flying insect enemies. However, exclusion of birds from treatments with other enemy guilds did not significantly impact mean aphid densities in any round (O vs. -B and -G vs. -G-B; Figure 3.1).

Combined effects of ground-dwellers and flying insects on aphid suppression were stronger than in isolation (Figure 3.1). On average, aphids were reduced 35% (26-51%) more in the presence of both guilds than with ground-dwellers alone, and 15% (6-22%) more than with flying insects alone. Overall, these guilds thus had complementary impacts on aphid suppression. However, aphid suppression was less strong in the presence of both guilds than if the effects

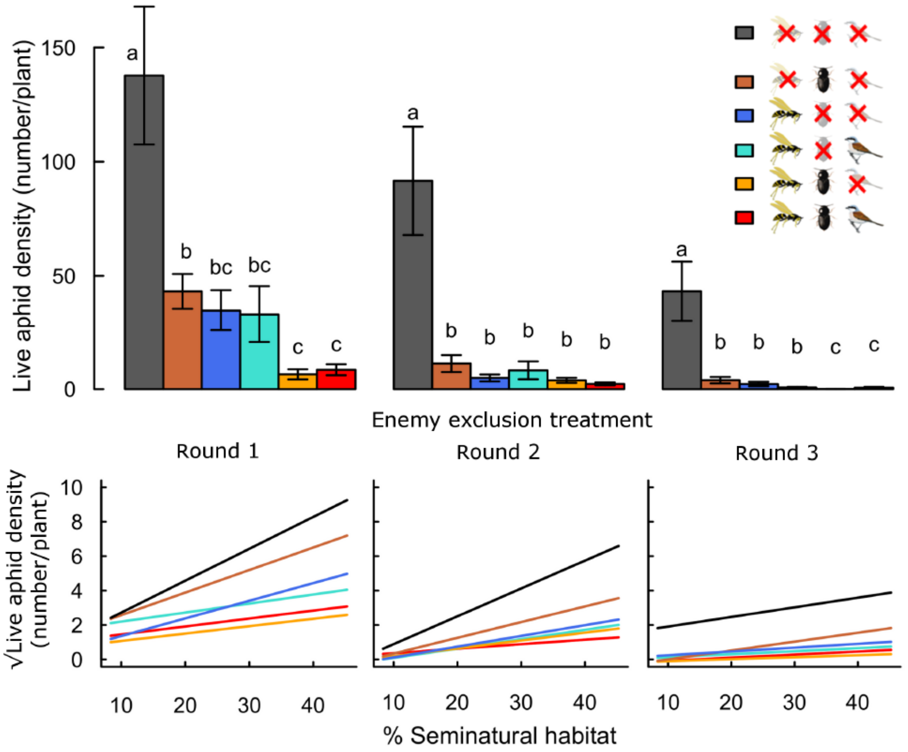

Figure 3.1. Effects of landscape complexity and natural enemy exclusion on aphid density in three sampling rounds (rounds 1-3; 10 day intervals). The top half of the figure shows mean densities ± s.e.m. per exclusion treatment and round. The lower half shows variation of predicted square root-transformed values across the gradient in landscape complexity, measured by percent seminatural habitat in a 700 m radius around fields. Data points per treatment and round are provided in Figure S3.2. See Table S3.2 for multiple slope comparisons. Different letters indicate significant differences between treatments. In the legend, crossed-out symbols indicate exclusion of natural enemy functional guilds. Treatments remain accessible to non-excluded guilds. Guilds of natural enemies include flying insects (parasitoids, syrphid flies and predatory wasps; wasp symbol), ground-dwellers (carabid beetles, staphylinids and spiders; beetle symbol) and birds (and other vertebrates larger than 1.5 cm; bird symbol).

of these guilds had added up, thus indicating either a sub-additive but complementary interaction, or limitation of additivity by low aphid densities.

Aphid density in controls excluding all natural enemies increased 5.5±2.6-fold with the proportion of seminatural habitat in the surrounding landscape (mean±s.e.m across rounds; Figures 3.1, S3.2; Table S3.2: -G-F-B vs. zero, $p_{adjusted}<0.05$ in rounds 1 & 2). However, the degree of aphid suppression by natural enemies also increased with landscape complexity (landscape:treatment interaction; Tables 3.1, S3.2), and these effects were maintained across several spatial scales (Table S3.1). At the 700 m scale around fields, aphid suppression by all natural enemies (the difference between densities in the absence and in the presence of all enemies) was 6±2.5 times higher in complex than in simple landscapes (mean ± s.e.m. across rounds; Table S3.2: -G-F-B vs. O). Differences between aphid density in controls excluding enemies, and in treatments accessible to flying insects, were also stronger in complex than in simple landscapes, thus aphid suppression by the guild of flying insects also increased with landscape complexity (Table S3.2: -G-F-B vs. -G-B). This effect was maintained and even increased when flying insects were combined with ground-dwellers and birds. However, effects of ground-dwellers only (the difference between treatments with ground-dwellers only and controls without enemies) were less strong across the landscape gradient than effects of flying insects (Table S3.2: -G-F-B vs. -F-B). Thus, particularly in complex landscapes, flying insect

Table 3.1 Results of model selection relating landscape complexity and enemy exclusion to response variables. Model lists show the 95% best models at the most predictive scale for each response variable. w: AIC weight compared to all possible models, w95%: AIC weight within the 95% model confidence set. The sum of weights for each term is the sum of AIC weights of all models selecting it and represents the probability of being present in the 95% model confidence set. Explanatory variables are M: management of the nearest surrounding field (organic / conventional); L: landscape complexity (percent seminatural habitat in the most predictive radius); R: sampling round (1-3); T: exclusion treatment (6 levels of natural enemy exclusion).

Response	n°	Model specification									df	AICc	ΔAIC	w	w 95%
sqrt(aphid density) ~	M1	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5641.3	0	0.482	0.512
	M2	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5642.9	1.62	0.215	0.228
	M3	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5643.3	2.02	0.176	0.187
	M4	M +	L +	R +	T +	M:R +	L:R				26	5645.2	3.92	0.068	0.072
Sum of weights		***0.97***	***1***	***1***	***1***	***1***	***1***	***0.93***	***0.7***	***0.51***				0.941	1
parasitism rate ~	M5	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	43	1075.9	0	0.643	0.7
	M6	M +	L +	R +	T +	M:R +	L:R +	T:R			28	1078.5	2.64	0.172	0.187
	M7	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		33	1079.5	3.64	0.104	0.114
Sum of weights		***0.95***	***1***	***1***	***1***	***1***	***1***	***1***	***0.81***	***0.7***				0.919	1
syrphid:aphid ratio ~	M8	M +	L +	R +	T +	M:R +	L:R +		L:T		23	854.8	0	0.633	0.686
	M9	M +	L +	R +	T +	M:R +			L:T		21	856.7	1.95	0.239	0.259
	M10	M +	L +	R +	T +	M:R +	L:R +				18	859.8	5.03	0.051	0.056
Sum of weights		***1***	***1***	***1***	***1***	***1***	***0.74***		***0.94***					0.923	1
aphid population growth ~	M11	M									5	1442.6	0	0.368	0.425
	M12	M +	L								6	1443	0.33	0.312	0.361
	M13		L								5	1444	1.38	0.184	0.213
Sum of weights		***0.79***	***0.57***											0.864	1

enemies reduced aphids 1.4 (rounds 2 and 3 at low aphid densities) to 2 times (round 1 at high aphid densities) more than ground-dwelling predators (on average across rounds: 61±8% vs. 40.5±9% reduction compared to controls for flying insects and ground-dwellers, respectively; mean±s.e.m.).

Effects of enemy exclusion and landscape context on enemy:aphid ratios

Rates of parasitism and syrphid:aphid ratios were higher in treatments accessible to flying insects than in treatments excluding them, confirming the effectiveness of exclosures for these enemies (Figure 3.2, Table 3.1). These differences were significant for parasitism rates and less strong for syrphid:aphid ratios, as only low numbers of syrphid larvae (on average 0.3±0.03 in accessible treatments) were recorded per plant. Rates of parasitism and syrphid:aphid ratios increased with landscape complexity at the 1000 m scale around fields, particularly in treatments accessible only to this guild (flying insects) (Figure 3.2; Table S3.2: -G-B vs. zero). However, although aphid reduction was strong in complex landscapes when flying insects were combined with other guilds (Figure 3.1), this was not reflected by high rates of parasitism in treatments combining several guilds (Figure 3.2A). Indeed, rates of parasitism were lower when flying insects were combined with ground-dwellers or birds (treatments -G, -B, O). In contrast, syrphid:aphid ratios were less affected than parasitoids by the presence of ground-dwellers (-G-B vs. -B: in round 1, $p = 0.058$ for parasitism rates and $p = 0.318$ for syrphid:aphid ratios; Table S3.2).

Although birds had no clear effects on aphid densities, parasitism rates and syrphid:aphid ratios indicate that they interacted with these enemies. In the presence of flying insects and birds, syrphid:aphid ratios were significantly lower than with flying insects only (-G-B vs. -G; $p_{adjusted} = 0.012$ in round 1; Table S3.2). However, in open treatments with ground-dwellers also present, a negative effect of birds on syrphid:aphid ratios was not found (-G-B vs. O; $p_{adjusted} = 0.207$ in round 1; Table S3.2).

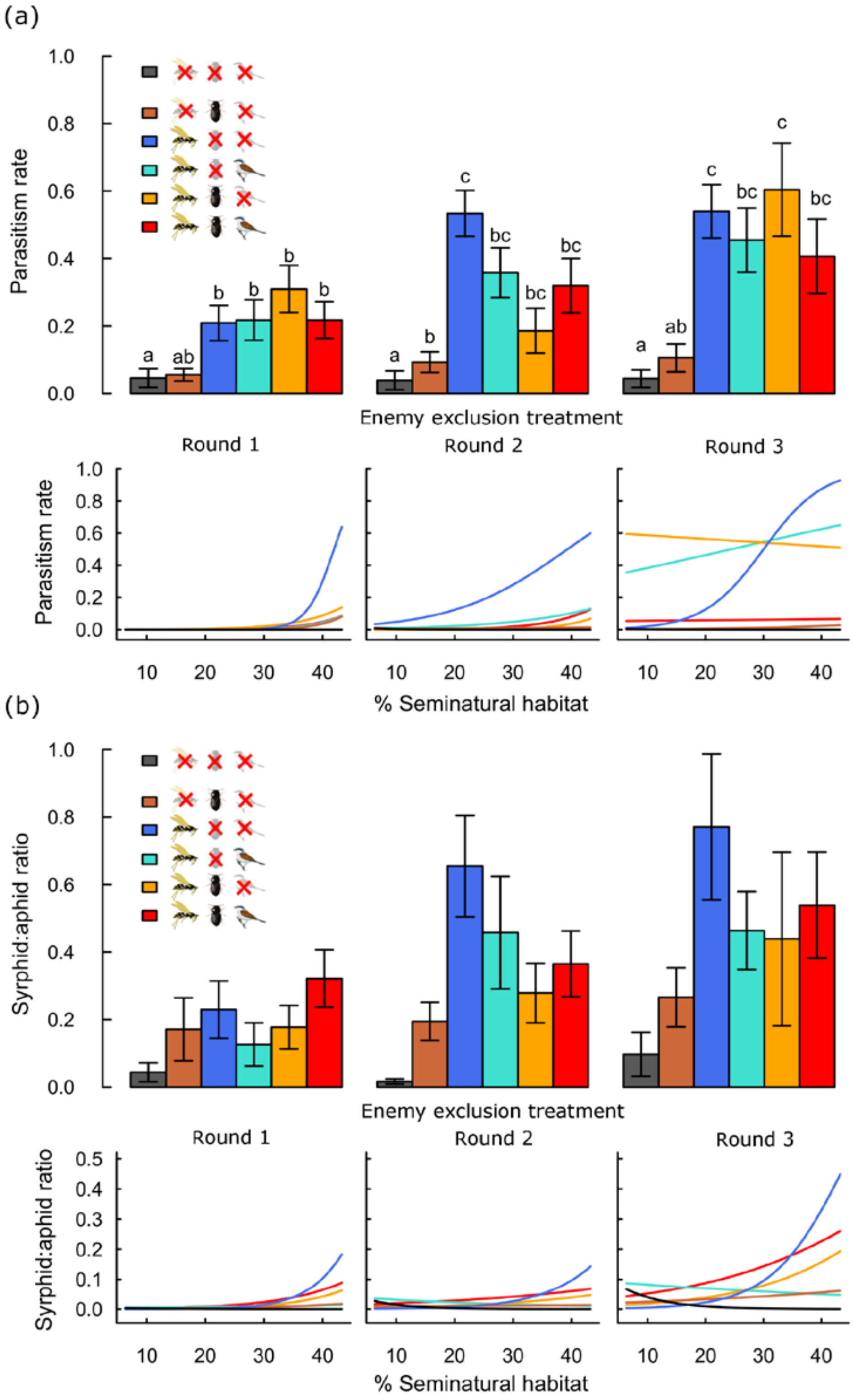

Figure 3.2 Effects of landscape complexity and natural enemy exclusion on (a) aphid parasitism rate and (b) syrphid:aphid ratio in three sampling rounds (rounds 1-3; 10 day intervals). The top half of each figure shows mean values ± s.e.m. per exclusion treatment and round. The lower half shows variation of predicted values across the gradient in landscape complexity, measured by percent seminatural habitat in a 1 km radius around fields. Data points per treatment and round are provided in Figures S3.3, S3.4. See Table S3.2 for slope multiple comparisons. Different letters indicate significant differences between treatments. Detailed legend description is provided in Figure 3.1.

Aphid population growth and yields

Aphid populations were highest in round 1 and decreased in the following rounds (Figure 3.1). Effects of exclusion treatment on aphid population growth were not significant. However, all treatments combined, population growth was negatively affected by landscape complexity (Figure 3.3, Table 3.1), with populations decreasing ca. 42% more in complex compared to simple landscapes. In addition, aphid population growth was negatively correlated with parasitism rate and syrphid:aphid ratio (Figure 3.4, $p<0.001$ and $p=0.003$, respectively), thus confirming the impact of these enemies for reduction of aphid populations. On average, aphid populations remained below positive growth thresholds for the duration of sampling rounds, even after initial population build-up in the course of round 1 (Figures 3.3, 3.4).

Neither aphid population growth across rounds, nor aphid density in each round led to a significant decrease in final crop biomass. However, densities of syrphid larvae were strongly positively related to increasing crop biomass (Figure 3.4, $p<0.001$), thus showing a direct positive link between the abundance of syrphid predators and the provision of yields. In contrast, parasitoid density did not significantly affect crop biomass ($F = 1.36$, $p = 0.25$).

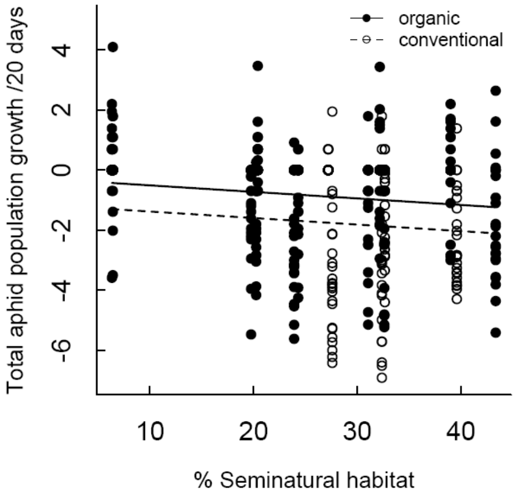

Figure 3.3 Effect of landscape complexity (1 km radius) and management intensity on aphid population growth, quantified as the log ratio of aphid density in sampling rounds 3 and 1 (20 days apart). Regression lines show model-averaged predicted values. See statistics in Table 3.1. Full points and solid lines: organic, open points and dashed lines: conventional management of the nearest surrounding field.

Management effects

Particularly in round 1, aphid densities were higher in plots surrounded by conventional than by organic fields (Figure S3.2; Table 3.1). However, no difference was found in subsequent rounds (Figure S3.2). Aphid populations thus decreased more strongly from round 1 to round 3 in fields surrounded by conventional than by organic fields (Figure 3.3). In contrast, enemy:aphid ratios were similar in both management types in round 1, but higher near conventional fields in the following rounds (Figures S3.3, S3.4).

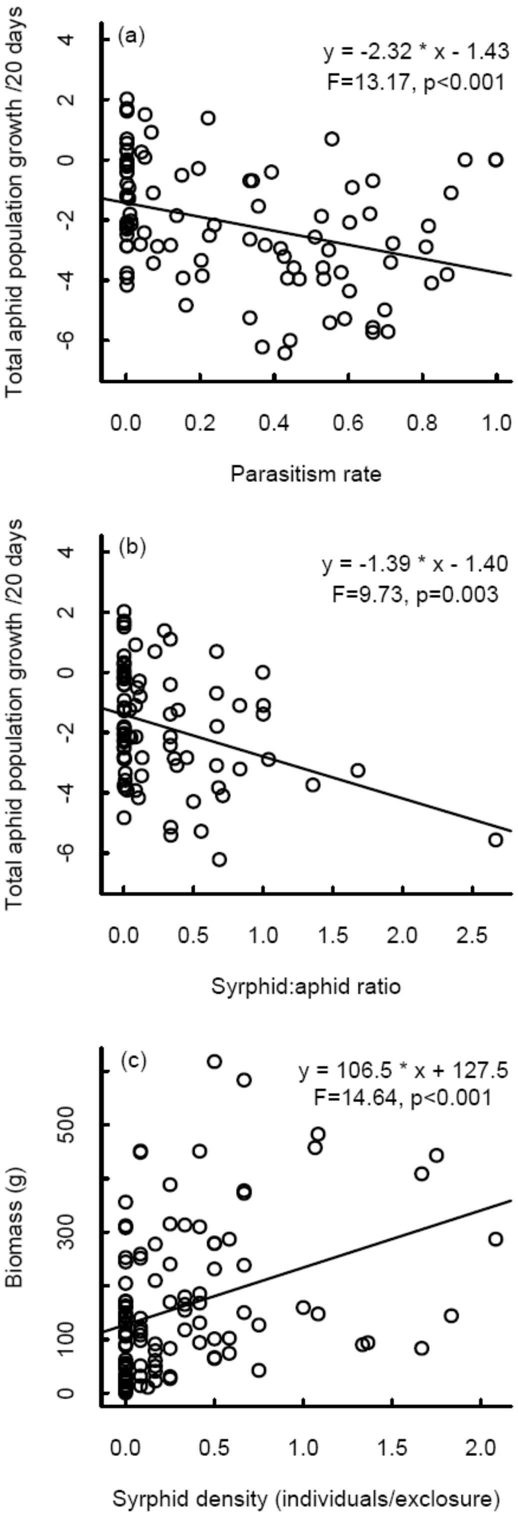

Figure 3.4 Relationship between total aphid population growth and (a) parasitism rate, (b) syrphid:aphid ratio and (c) between final cabbage biomass (mean/exclosure) and syrphid larval density. Parasitism (n = 97) and syrphid:aphid ratio (n = 82) are means of rounds. Syrphid density is the mean of plants and rounds/exclosure (n = 108).

3.4. Discussion

Pest density and pest control across the landscape gradient

This study shows that in the absence of pressure by natural enemies, aphid pest densities increased with landscape complexity at several spatial scales. However, aphid pests were also strongly reduced by natural enemies, and this pest reduction increased with landscape complexity. Overall, aphid densities were thus maintained at low levels in all landscapes, due to compensation of higher aphid colonization in complex landscapes by stronger pressure by natural enemies.

An increase of aphid densities with landscape complexity can be explained by higher availability of alternative resources and overwintering habitats in seminatural areas surrounding fields (Bianchi et al., 2006). Although several studies have measured the distribution of pest abundance across landscapes, results remain inconclusive, as pests appear to either decrease, increase or not to vary with landscape complexity (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). However, only a few recent studies have measured landscape effects on pests in the absence vs. in the presence of natural enemies and thus provide measures of actual pest pressure across landscapes (Gardiner et al., 2009; Thies et al., 2011; Chaplin-Kramer and Kremen, 2012; Holland et al., 2012; Martin et al., 2013; Rusch et al., 2013). Only three of these report results of pest variation separately from an aggregated measure of pest control, with pest pressure either increasing with landscape complexity as shown here (Chaplin-Kramer and Kremen, 2012; Martin et al., 2013) or decreasing with combined landscape and local extensification (Thies et al., 2011). The lack of general patterns highlights the fact that pest densities are affected by the landscape both directly and indirectly through landscape effects on higher trophic levels (enemies) and emphasizes the need to experimentally address these factors in isolation from each other.

In agreement with our results, the few studies measuring actual pest control of aphids as the difference between pest density in the presence and in the absence of natural enemies, also find increasing intensity of pest control with the proportion of natural or seminatural habitats in the surrounding landscape. The strength of aphid pest control increased in these studies by a factor of 2 to 5 from simple to complex landscapes (Gardiner et al., 2009; Chaplin-Kramer and Kremen, 2012; Rusch et al., 2013), and was here on average 6 times higher in complex than in simple landscapes. So far, however, no other study has disentangled the single and combined contributions of antagonist guilds including birds to aphid pest control along a landscape complexity gradient.

Enemy contributions to pest control and interactions

On average, ground-dwellers and flying insect enemies had similar impacts on aphid control. However, effects of flying insects increased in complex landscapes, paralleling their generally higher abundance and species richness in landscapes with high amounts of seminatural habitat, than in simple ones where overwintering, nesting, and food resources are rare (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). The importance of landscape complexity for flying insect effectiveness is confirmed by increased activity rates (parasitism and syrphid:aphid ratios) of this guild in complex landscapes, both here and in other studies (e.g., Thies and Tscharntke, 1999). Ground-dwellers, on the other hand, also showed stronger effects with increasing amounts of seminatural habitat, possibly reflecting higher ground-dweller diversity in complex landscapes (Geiger et al., 2010; but see Winqvist et al., 2011). However, control by ground-dwellers increased to a lesser extent with landscape complexity than control by flying insect enemies. Thus, the relative contribution of these guilds to pest suppression was influenced by the landscape context, and particularly in complex landscapes, specialized flying insects contributed more strongly to pest control than the more generalist ground-dweller enemies, in agreement with local-scale studies (Schmidt et al., 2003; Diehl et al., 2013) and with the idea that generalist predators have lower impacts than specialists when prey density is high (Straub et al., 2008). Birds, on the other hand, showed no clear contribution to reducing aphids in any landscape. Thus, not only does the guild of flying insect enemies generally show the most predictable responses to changes in landscape complexity (Bianchi et al., 2006): it is also the guild with the strongest impact on pests under favorable conditions of landscape complexity.

Strong impacts of the guild of flying insects are confirmed by the strong reduction of aphid population growth by parasitoids and syrphids. However, only syrphids had an impact on crop biomass, the final measure of interest for assessment of pest control. Ultimately, benefits for farmers may thus be higher when enemies are predators that immediately suppress pests, than when they are parasitoids with slower impacts on their hosts. Overall, flying insect enemies and particularly syrphid flies may represent an optimal focus for efforts to maximize natural pest control in agricultural landscapes. However, the effectiveness of these efforts depends on the balance between individual enemy contributions, and how they interact with other natural enemy guilds.

Interactions between flying insects and ground-dwellers led to complementary effects on pest control, as aphid suppression was stronger in the presence of both guilds than with either guild alone, in agreement with results in other aphid systems (Schmidt et al., 2003). This effect may be due to density-dependent predation by each guild, to their spatially segregated foraging (Straub et al., 2008), but also to escape behavior of aphids from flying insects increasing the chances of ground-dweller predation (Losey and Denno, 1998). Syrphid:aphid ratios show that syrphid larvae were little influenced by the presence of ground-dwellers and could thus suppress aphids independently of ground-dweller activity. However, lower parasitism rates in the presence of ground-dwellers (-G-B vs. -B) suggest that ground-dwellers preyed not only on live aphids, but also on parasitized mummies, particularly in complex landscapes where parasitoid activity was strong. Such effects have previously been observed in local-scale studies for carabid predators (Snyder and Ives, 2001) which form a substantial proportion of the ground-dwellers in this study. Partial competition for prey, particularly given low overall densities, but also intraguild predation of parasitoids by ground-dwellers, may thus have led to the complementary but sub-additive relationship between flying insect and ground-dweller guilds.

Birds, the largest predators in the system and the most generalist, appeared to interact in complex ways with aphids and other enemies. Although their effects have rarely been quantified in agricultural systems with annual crops (Mooney et al., 2010) and almost never in the light of interactions with other enemies (but see Hooks et al., 2003), birds are known to occasionally feed on aphids in these systems (Tremblay et al., 2001). Here, coincidental predation by birds of parasitized aphids in addition to live ones is consistent with the generalist foraging techniques of these enemies, which would not necessarily distinguish parasitized from non-parasitized aphids while foraging. The same logic applies to bird effects on syrphid larvae, as there should be no reason for birds not to prey on these larvae when already foraging for aphids on the same plants. The consequences, however, are different: coincidental predation of mummies may still decrease aphid densities, but omnivorous predation of syrphids should theoretically release the shared prey (Straub et al., 2008). Overall, effects on aphids may thus level out and, as found here, lead to no effect of birds on aphid densities in treatments with only birds and flying insects. As observed with other generalist predators (Koss and Snyder, 2005), the presence of an additional guild (ground-dwellers) acting as alternative prey may have released pests and predators including syrphids from bird predation pressure, and thus syrphid ratios in open treatments with all three guilds increased.

Overall, strong negative effects of intraguild predation on aphid suppression were not found, as aphids were reduced sufficiently by the combination of all guilds to remain at below-threshold levels in open treatments throughout the experiment, thus emphasizing that effects of natural enemies and particularly birds are pest organism-dependent (Martin et al., 2013). In the case of aphids, pest control provided by the combination of three natural enemy functional guilds was thus higher than pest control by individual guilds, and this result held true across increasing conditions of landscape complexity. These results support the idea that higher functional diversity may benefit ecosystem function and services across large spatial scales (Cardinale et al., 2006), for particular combinations of functions and guilds. However, consideration of additional guilds or different pests may greatly influence this relationship, as suggested by contrasting effects of enemy functional diversity on control of Lepidopteran pests, in the same experiment (Martin et al., 2013).

Natural enemies and pests in organic vs. conventional plots

In plots surrounded by conventional fields, soil nitrogen availability was higher than near organic fields (Martin et al., 2013) and is likely to be responsible for higher initial aphid population build-up in these in plots (Butler et al., 2012). More natural enemies were thus required near conventional fields to effectively constrain aphids to the same degree as near organic fields. Higher aphid densities in round 1, followed by no differences in subsequent rounds, suggest that a time lag took place near conventional fields before enemies reached sufficient densities to effectively reduce pests in these plots (Krauss et al., 2011), thus suggesting lower efficiency of early-stage pest control near conventional compared to organic fields.

3.5. Conclusion

Despite complex interactions occurring between enemy functional guilds across landscapes, pest control of aphids benefited in all landscapes from high enemy functional diversity, and was stronger in complex landscapes with high amounts of seminatural habitat than in simple ones. Pest control by flying insects and ground-dwellers was complementary, but flying insects including syrphids provided the strongest contributions to aphid pest control particularly in complex landscapes. These results emphasize the need to identify underlying interaction mechanisms of pest control at large spatial scales, in order to provide realistic predictions of ecosystem service provision in agricultural landscapes, and thus improve the applicability of this concept for higher agricultural sustainability.

3.6. Acknowledgements

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3.8. Supplementary Tables

Table S 3.1 Effect of scale on the response of aphid densities. Sets of 95% confidence models and weights of each explanatory variable are shown for square root-transformed aphid density at scales from 100 to 1000 m around fields. Lowest AIC values of the full model (not shown) and of selected models (in bold) were obtained at the 700 m scale. w: AIC weight compared to all possible models, w95%: AIC weight within the 95% model confidence set. Explanatory variables are M: management type of the nearest surrounding field (organic / conventional); L: landscape complexity (% seminatural habitat in the surrounding radius); R: sampling round (1-3); T: exclusion treatment (6 levels of natural enemy exclusion)

Scale of response	Model specification									df	AICc	ΔAIC	w	w 95%
100 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5653.5	0	1	1
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***1***					1	1
200 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5675.3	0	0.76	0.81
200 m	M +	L +	R +	T +	M:R +		T:R +	L:T		39	5678.3	2.92	0.18	0.19
Sum of weights	***1***	***1***	***1***	***1***	***1***	***0.81***	***1***	***1***					0.93	1
300 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5675.9	0	0.85	0.92
300 m	M +	L +	R +	T +	M:R +		T:R +	L:T		39	5680.8	4.91	0.07	0.08
Sum of weights	***1***	***1***	***1***	***1***	***1***	***0.92***	***1***	***1***					0.92	1
400 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5661.6	0	0.69	0.80
400 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5664.4	2.83	0.17	0.20
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***0.8***					0.86	1
500 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5657.5	0	0.66	0.70
500 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5659.7	2.15	0.23	0.24
500 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5662.6	5.01	0.05	0.06
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***0.3***	***0.06***				0.94	1
600 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5654	0	0.6	0.65
600 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5656	1.96	0.22	0.25
600 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5657.8	3.76	0.09	0.10
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***1***	***0.35***	***0.1***				0.91	1
700 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	**5641.3**	0	0.48	0.51
700 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	**5642.9**	1.62	0.22	0.23
700 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	**5643.3**	2.02	0.18	0.19
700 m	M +	L +	R +	T +	M:R +	L:R				26	**5645.2**	3.92	0.07	0.07
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***0.93***	***0.7***	***0.51***				0.94	1
800 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5664.3	0	0.35	0.38
800 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5664.8	0.46	0.28	0.30
800 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5665.6	1.25	0.19	0.20
800 m	M +	L +	R +	T +	M:R +	L:R				26	5666.5	2.17	0.12	0.13
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***0.87***	***0.5***	***0.3***				0.93	1
900 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5672.6	0	0.42	0.45
900 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5673.5	0.89	0.27	0.29
900 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T		41	5675	2.35	0.13	0.14
900 m	M +	L +	R +	T +	M:R +	L:R				26	5675.1	2.5	0.12	0.13
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***0.87***	***0.59***	***0.45***				0.94	1
1000 m	M +	L +	R +	T +	M:R +	L:R +	T:R +	L:T +	L:T:R	51	5680.8	0	0.63	0.68
1000 m	M +	L +	R +	T +	M:R +	L:R +	T:R			36	5683.1	2.31	0.2	0.21
1000 m	M +	L +	R +	T +	M:R +	L:R				26	5684.4	3.66	0.1	0.11
Sum of weights	***1***	***1***	***1***	***1***	***1***	***1***	***0.89***	***0.68***	***0.68***				0.93	1

Table S 3.2 Multiple comparisons of slopes for A) aphid density, B) parasitism rate, C) syrphid:aphid ratio in three sampling rounds. Treatments are *O*: open treatment without exclusion; *-B*: exclusion of birds; *-G*: exclusion of ground-dwellers; *-G-B*: exclusion of ground-dwellers and birds, but not flying insects; *-F-B*: exclusion of flying insects and birds; *-G-F-B*: control excluding all enemies but including herbivores. P-values are adjusted for the False Discovery Rate. Significance codes are '***' p<0.001, '**' p<0.01, '*' p<0.05, '.' p<0.1

A. Aphid density	**Sampling round 1**					**Sampling round 2**					**Sampling round 3**				
Treatments	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)
-G-F-B vs. zero	0.27	0.1	2.7	0.007 **	0.039 *	0.24	0.07	3.65	0 ***	0.003 **	0.06	0.04	1.68	0.094 .	0.323
-G-F-B vs. -F-B	-0.37	0.21	-1.78	0.075 .	0.11	-0.37	0.13	-2.73	0.006 **	0.017 *	-0.06	0.07	-0.8	0.423	0.676
-G-F-B vs. -G-B	-0.41	0.21	-1.99	0.047 *	0.075 .	-0.41	0.13	-3.06	0.002 **	0.007 **	-0.1	0.07	-1.38	0.168	0.323
-G-F-B vs. -G	-0.5	0.21	-2.44	0.015 *	0.039 *	-0.42	0.13	-3.15	0.002 **	0.007 **	-0.11	0.07	-1.44	0.15	0.323
-G-F-B vs. -B	-0.52	0.2	-2.54	0.011 *	0.039 *	-0.43	0.13	-3.28	0.001 **	0.006 **	-0.11	0.07	-1.56	0.118	0.323
-G-F-B vs. O	-0.51	0.2	-2.51	0.012 *	0.039 *	-0.47	0.13	-3.57	0 ***	0.003 **	-0.1	0.07	-1.41	0.159	0.323
-F-B vs. -G-B	0.04	0.06	0.64	0.522	0.642	0.04	0.04	0.93	0.354	0.436	0.04	0.03	1.34	0.182	0.323
-F-B vs. -G	0.13	0.06	2.15	0.032 *	0.06 .	0.05	0.04	1.19	0.234	0.312	0.05	0.03	1.49	0.138	0.323
-F-B vs. -B	0.15	0.06	2.68	0.007 **	0.039 *	0.07	0.04	1.64	0.102	0.181	0.06	0.03	1.82	0.068 .	0.323
-F-B vs. O	0.14	0.06	2.53	0.011 *	0.039 *	0.11	0.04	2.57	0.01 *	0.023 *	0.04	0.03	1.44	0.15	0.323
-G-B vs. -G	0.09	0.06	1.7	0.089 .	0.119	0.01	0.04	0.29	0.776	0.776	0	0.03	0.15	0.88	0.959
-G-B vs. -B	0.11	0.05	2.3	0.022 *	0.05 *	0.02	0.04	0.69	0.488	0.557	0.01	0.03	0.45	0.656	0.906
-G-B vs. O	0.1	0.05	2.13	0.033 *	0.06 .	0.06	0.04	1.75	0.08 .	0.16	0	0.03	0.05	0.959	0.959
-G vs. -B	0.02	0.05	0.33	0.744	0.851	0.01	0.04	0.38	0.704	0.751	0.01	0.03	0.29	0.774	0.952
-G vs. O	0.01	0.05	0.2	0.839	0.887	0.05	0.04	1.45	0.147	0.234	0	0.03	-0.11	0.915	0.959
-B vs. O	-0.01	0.04	-0.14	0.887	0.887	0.04	0.03	1.24	0.216	0.312	-0.01	0.03	-0.41	0.679	0.906

Table S 3.2 (continued)

B. Parasitism rate	**Sampling round 1**					**Sampling round 2**					**Sampling round 3**				
Treatments	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)
-G-F-B vs. zero	-0.21	0.15	-1.37	0.17	0.303	-0.26	0.15	-1.68	0.093 .	0.297	-0.17	0.12	-1.4	0.162	0.532
-F-B vs. zero	0.49	0.2	2.44	0.015 *	0.092 .	0.27	0.21	1.27	0.205	0.546	0.24	0.19	1.26	0.208	0.532
-G-B vs. zero	0.71	0.21	3.42	0.001 ***	0.01 *	0.35	0.19	1.81	0.07 .	0.281	0.4	0.17	2.36	0.018 *	0.289
-G vs. zero	0.43	0.18	2.38	0.017 *	0.092 .	0.34	0.18	1.88	0.06 .	0.281	0.2	0.15	1.37	0.171	0.532
-B vs. zero	0.34	0.19	1.78	0.075 .	0.201	0.51	0.21	2.39	0.017 *	0.137	0.14	0.17	0.79	0.428	0.699
O vs. zero	0.39	0.19	2.07	0.038 *	0.152	0.45	0.19	2.38	0.017 *	0.137	0.16	0.15	1.09	0.275	0.549
-F-B vs. -G-B	-0.22	0.21	-1.07	0.286	0.457	-0.08	0.2	-0.39	0.696	0.8	-0.16	0.21	-0.78	0.437	0.699
-F-B vs. -G	0.06	0.19	0.31	0.757	0.789	-0.07	0.19	-0.38	0.708	0.8	0.04	0.19	0.23	0.819	0.874
-F-B vs. -B	0.15	0.19	0.79	0.431	0.627	-0.24	0.22	-1.09	0.276	0.631	0.11	0.21	0.5	0.618	0.874
-F-B vs. O	0.1	0.19	0.55	0.585	0.72	-0.18	0.2	-0.88	0.378	0.668	0.08	0.19	0.43	0.664	0.874
-G-B vs. -G	0.28	0.19	1.46	0.145	0.29	0.01	0.17	0.03	0.977	0.977	0.21	0.17	1.19	0.233	0.532
-G-B vs. -B	0.37	0.2	1.89	0.058 .	0.186	-0.16	0.2	-0.81	0.417	0.668	0.27	0.19	1.39	0.164	0.532
-G-B vs. O	0.32	0.19	1.67	0.096 .	0.218	-0.1	0.18	-0.56	0.579	0.772	0.25	0.17	1.41	0.158	0.532
-G vs. -B	0.09	0.17	0.55	0.584	0.72	-0.17	0.19	-0.88	0.382	0.668	0.06	0.17	0.37	0.714	0.874
-G vs. O	0.05	0.17	0.27	0.787	0.789	-0.1	0.17	-0.62	0.537	0.772	0.04	0.14	0.28	0.781	0.874
-B vs. O	-0.05	0.18	-0.27	0.789	0.789	0.06	0.2	0.32	0.75	0.8	-0.02	0.17	-0.13	0.897	0.897

C. Syrphid: aphid ratio	**Sampling round 1**					**Sampling round 2**					**Sampling round 3**				
Treatments	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)	Estimate	SE	z value	p	p (adjusted)
-G-F-B vs. zero	-0.15	0.1	-1.43	0.153	0.245	-0.31	0.1	-2.96	0.003 **	0.025 *	-0.14	0.06	-2.15	0.032 *	0.157
-F-B vs. zero	0.29	0.12	2.36	0.018 *	0.09 .	0.34	0.12	2.69	0.007 **	0.026 *	0.07	0.09	0.8	0.427	0.569
-G-B vs. zero	0.41	0.13	3.18	0.001 **	0.012 *	0.38	0.12	3.07	0.002 **	0.025 *	0.29	0.1	2.73	0.006 **	0.102
-G vs. zero	0.07	0.11	0.63	0.532	0.655	0.2	0.11	1.81	0.07 .	0.17	0.08	0.08	1.02	0.31	0.454
-B vs. zero	0.27	0.15	1.88	0.06 .	0.137	0.32	0.12	2.64	0.008 **	0.026 *	0.27	0.12	2.26	0.024 *	0.157
O vs. zero	0.25	0.12	2.15	0.032 *	0.098 .	0.34	0.12	2.83	0.005 **	0.025 *	0.14	0.09	1.45	0.148	0.296
-F-B vs. -G-B	-0.12	0.11	-1.12	0.264	0.383	-0.04	0.11	-0.4	0.687	0.86	-0.22	0.11	-1.97	0.049 *	0.157
-F-B vs. -G	0.22	0.09	2.28	0.023 *	0.09 .	0.13	0.1	1.31	0.19	0.337	-0.01	0.09	-0.1	0.917	0.917
-F-B vs. -B	0.01	0.13	0.09	0.927	0.927	0.01	0.11	0.13	0.895	0.955	-0.2	0.12	-1.61	0.107	0.26
-F-B vs. O	0.04	0.1	0.39	0.695	0.794	0	0.11	-0.03	0.98	0.98	-0.07	0.1	-0.66	0.511	0.623
-G-B vs. -G	0.34	0.1	3.33	0.001 ***	0.012 *	0.18	0.1	1.78	0.075 .	0.17	0.21	0.11	1.97	0.049 *	0.157
-G-B vs. -B	0.14	0.14	1	0.318	0.425	0.06	0.11	0.54	0.587	0.854	0.02	0.13	0.15	0.878	0.917
-G-B vs. O	0.16	0.1	1.57	0.116	0.207	0.04	0.1	0.39	0.698	0.86	0.15	0.12	1.29	0.198	0.353
-G vs. -B	-0.2	0.12	-1.66	0.098 .	0.196	-0.12	0.1	-1.21	0.226	0.362	-0.19	0.12	-1.58	0.114	0.26
-G vs. O	-0.18	0.09	-2.09	0.037 *	0.098 .	-0.13	0.09	-1.43	0.154	0.309	-0.06	0.1	-0.61	0.545	0.623
-B vs. O	0.03	0.13	0.21	0.836	0.892	-0.02	0.1	-0.16	0.871	0.955	0.13	0.13	1.01	0.312	0.454

3.9. Supplementary Figures

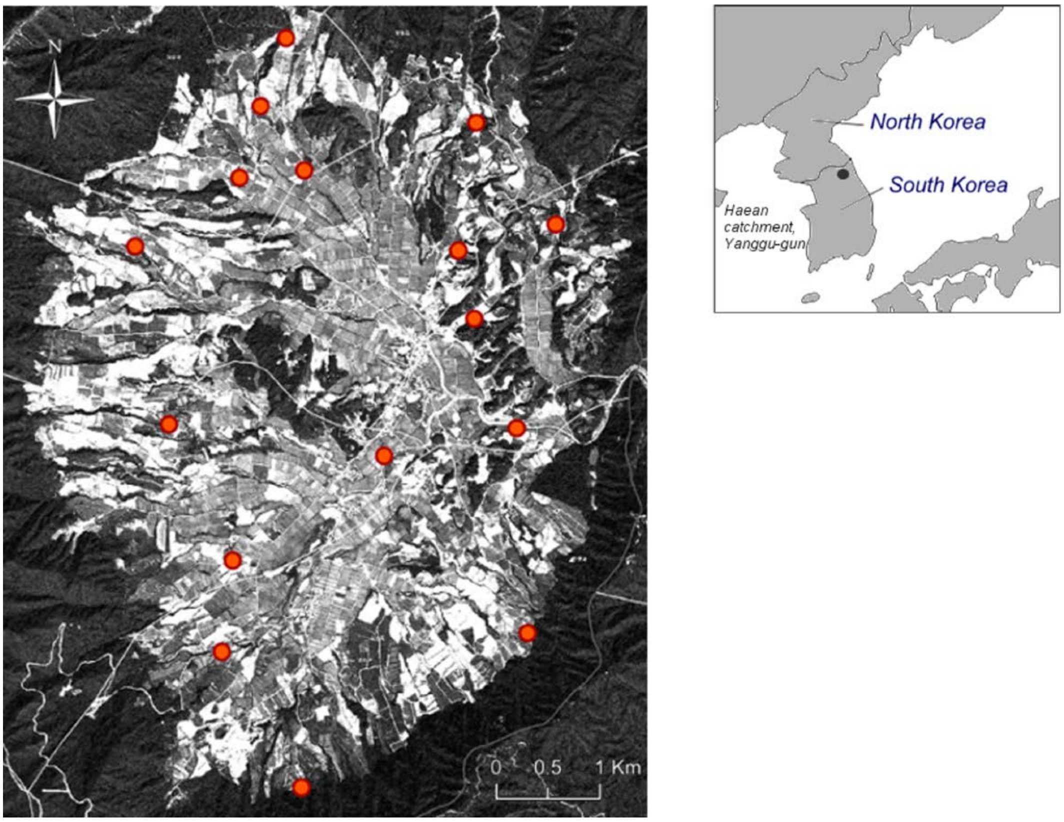

Figure S 3.1 Location of the Haean agricultural landscape (South Korea) and of 16 experimental cabbage plots (red dots; 2 plots outside the catchment are not shown). Satellite image modified from Cnes/Spot Image (Google Maps ©2013).

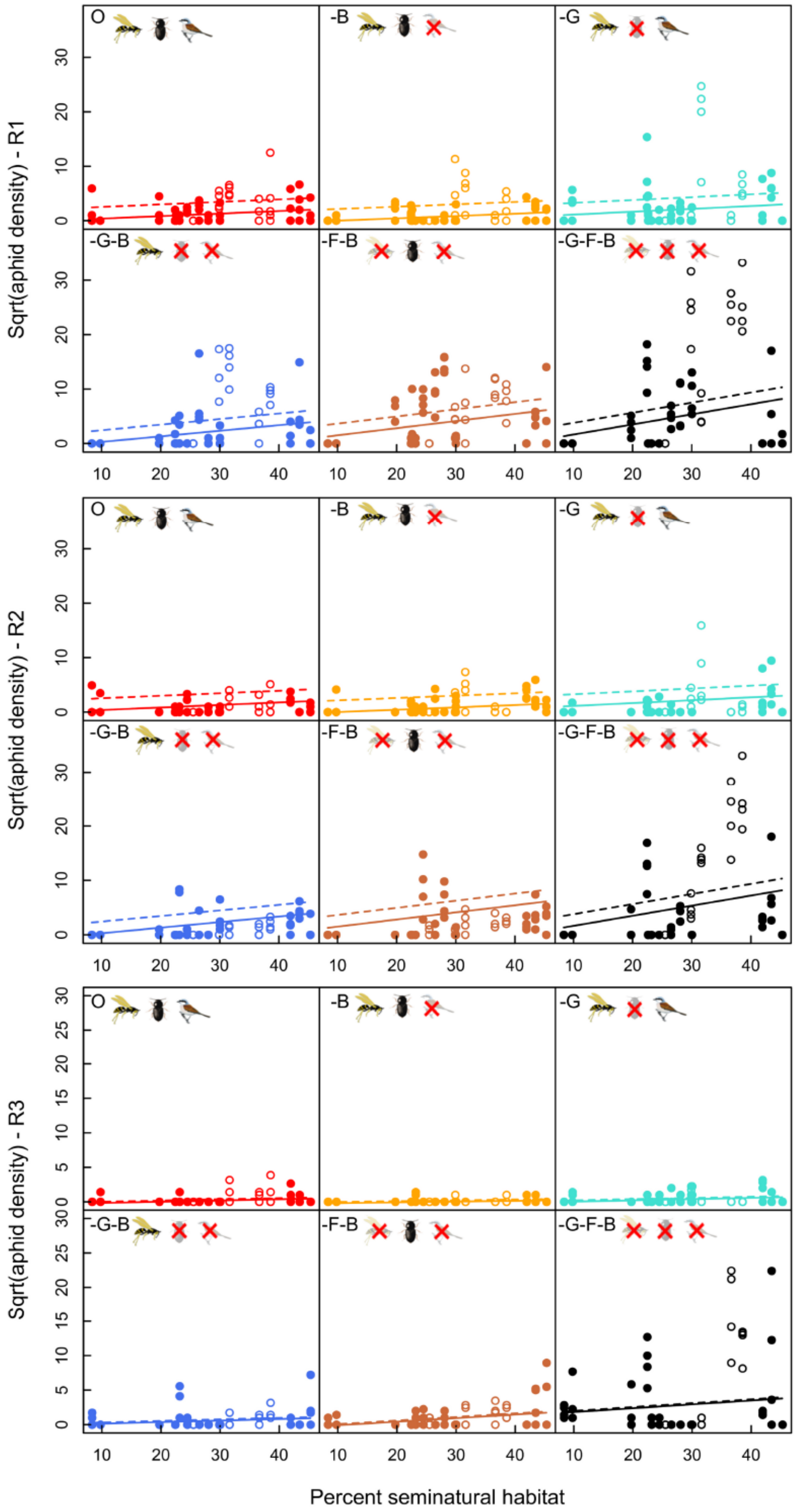

Figure S 3.2 Effects of landscape complexity and management type of the nearest surrounding field on square root-transformed aphid density, in 6 natural enemy exclusion treatments and 3 sampling rounds (R1-3) (n = 1272). Data points are given per round and treatment. Regression lines represent predicted model-averaging results. Landscape complexity is defined as % seminatural habitat in a 700 m radius around plots (results at other scales are shown in Table S3.1). Full points and solid lines: organic management of the nearest surrounding field (13 plots), open points and dashed lines: conventional management of the nearest surrounding field (5 plots). O: open treatment without exclusion; -G: exclusion of ground-dwellers; -B: exclusion of birds; -F-B: exclusion of flying insects and birds; -G-B: exclusion of ground-dwellers and birds, but not flying insects; -G-F-B: control excluding all enemies but including herbivores.

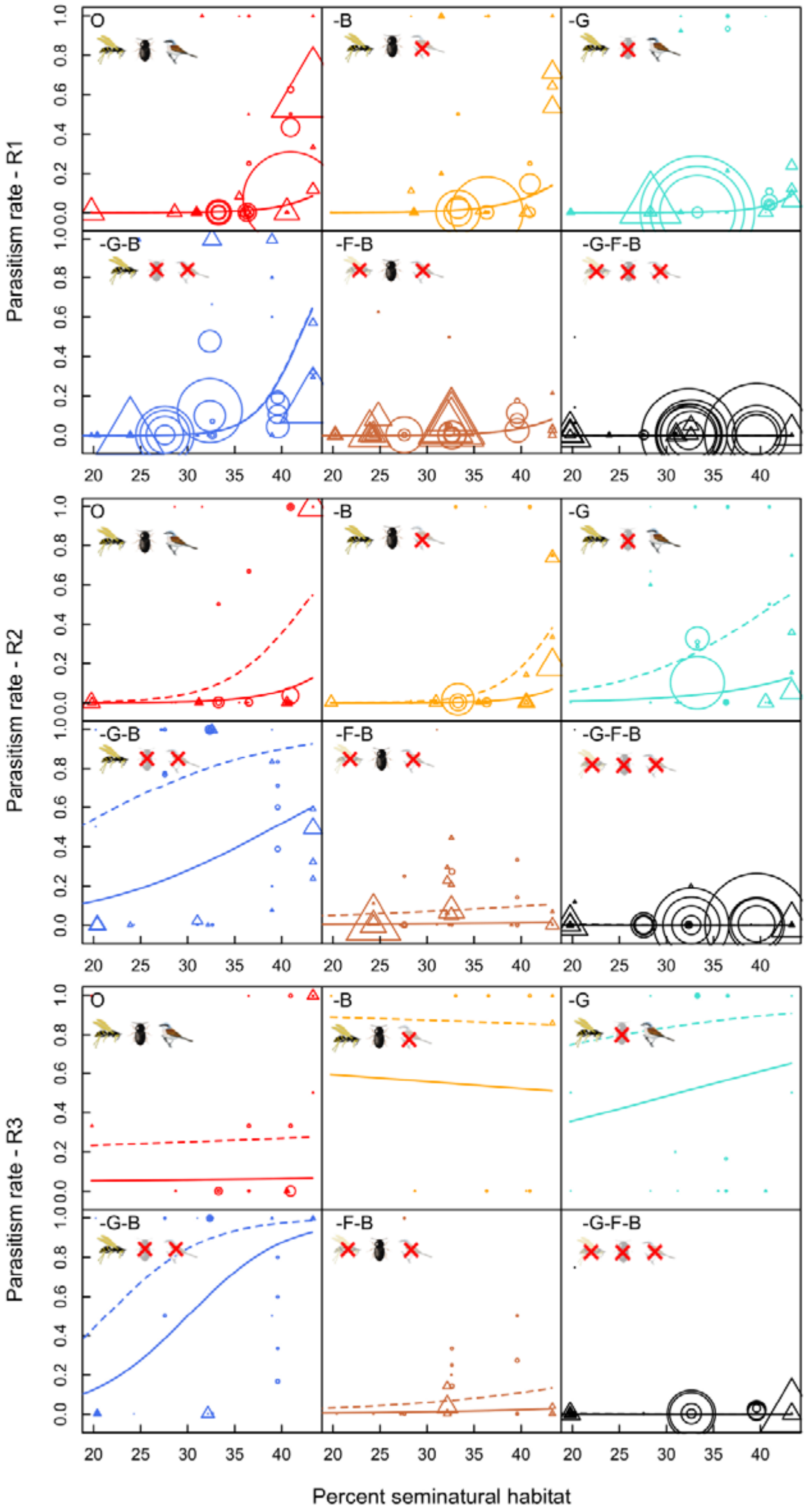

Figure S 3.3 Effects of landscape complexity and management type of the nearest surrounding field on aphid parasitism rate, in 6 natural enemy exclusion treatments and 3 sampling rounds (R1-3) (n = 1272). Data points are given per round and treatment. The area of each symbol is proportional to the total number of (parasitized + non-parasitized) aphids in the corresponding ratio of parasitized/total aphids. Regression lines represent predicted model-averaging results of binomial GLMMs. Landscape complexity is defined as % seminatural habitat in a 1000 m radius around plots (the most predictive scale of analysis for this response). Triangles and solid lines: organic management of the nearest surrounding field (13 plots), circles and dashed lines: conventional management of the nearest surrounding field (5 plots). O: open treatment without exclusion; -G: exclusion of ground-dwellers; -B: exclusion of birds; -F-B: exclusion of flying insects and birds; -G-B: exclusion of ground-dwellers and birds, but not flying insects; -G-F-B: control excluding all enemies but including herbivores.

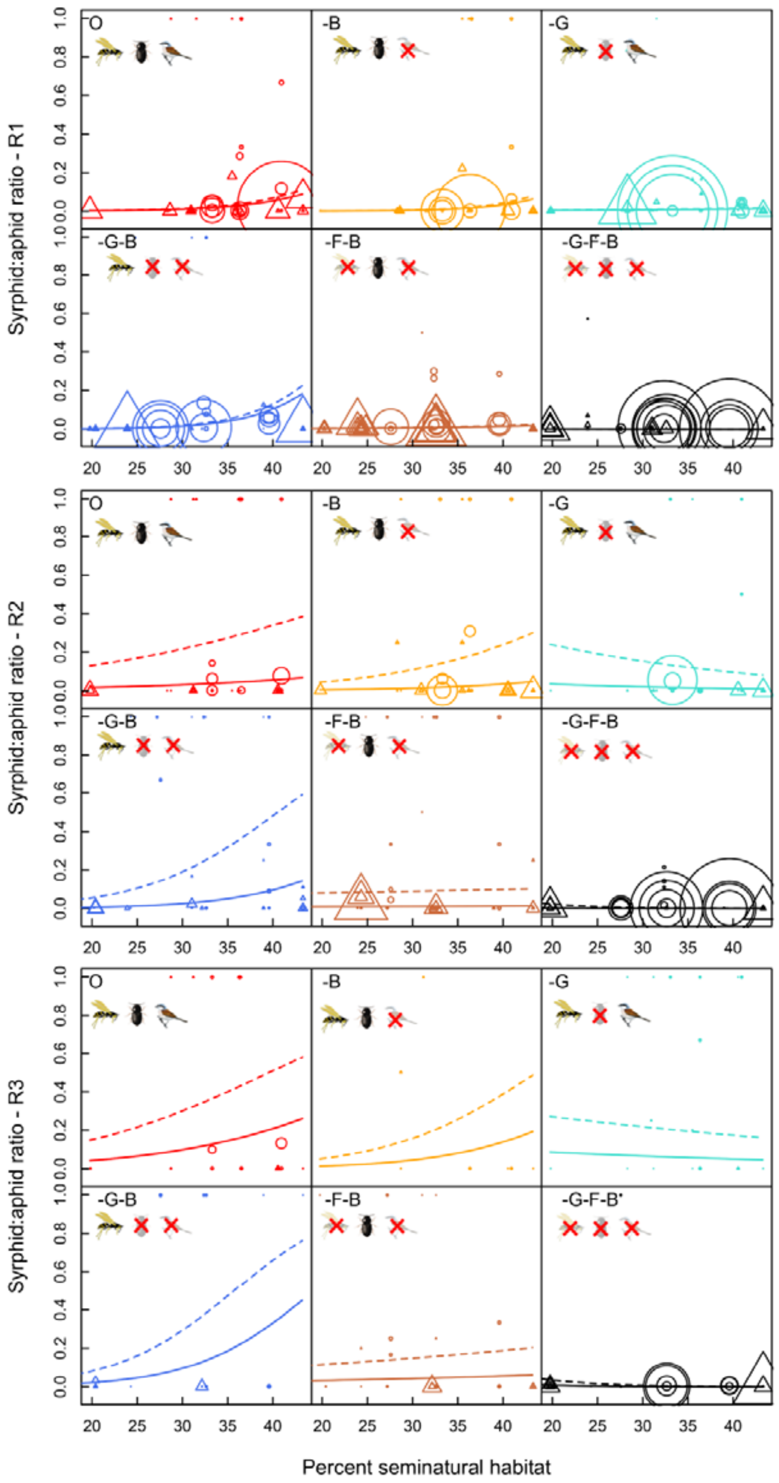

Figure S 3.4 Effects of landscape complexity and management type of the nearest surrounding field on syrphid:aphid ratios, in 6 natural enemy exclusion treatments and 3 sampling rounds (R1-3) (n = 1272). Data points are given per round and treatment. The area of each symbol is proportional to the total number of syrphids + aphids in the corresponding ratio of syrphids/aphids. Regression lines represent predicted model-averaging results of binomial GLMMs. Landscape complexity is defined as % seminatural habitat in a 1000 m radius around plots (the most predictive scale of analysis for this response). Triangles and solid lines: organic management of the nearest surrounding field (13 plots), circles and dashed lines: conventional management of the nearest surrounding field (5 plots). O: open treatment without exclusion; -G: exclusion of ground-dwellers; -B: exclusion of birds; -F-B: exclusion of flying insects and birds; -G-B: exclusion of ground-dwellers and birds, but not flying insects; -G-F-B: control excluding all enemies but including herbivores

Part 2

Chapter 4

4. Scale-dependent effects of landscape configuration and composition on natural enemy diversity and biological pest control

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Abstract

Pests and their natural enemies are influenced by the structure of landscapes and the intensity of local management. However, no study has disentangled the relative importance of landscape composition, configuration and diversity for multiple enemy groups across landscape-level spatial scales. Here, we show for the first time that positive effects of landscape structure across scales are driven for most enemies by the configuration of habitats around fields. In contrast, landscape composition, i.e. habitat amount and diversity, had both positive and negative effects on enemies across scales. Effects of local management intensity rarely interacted with landscape context. High enemy diversity was not reflected by low crop damage, indicating that other factors influence final pest control. Our results suggest that the effectiveness of agri-environmental schemes for managing natural enemy diversity and pest control could be enhanced by optimizing the effects of distinct landscape parameters across multiple landscape-level scales.

Keywords

Biological pest control, crop biomass, ecosystem services, herbivory, insect diversity, landscape configuration, landscape heterogeneity, land use intensification, spatial scales.

4.1. Introduction

Worldwide, landscapes are modified by human activities, particularly for the benefit of agriculture (Foley et al., 2005). By destroying natural and seminatural habitats and impacting species distributions, these modifications are likely to constrain the provision of ecosystem services essential to agriculture, such as biological pest control (Chapin III et al., 2000; Foley et al., 2005; Tscharntke et al., 2012). Pest control by natural enemies is valued at $13 billion in the United States alone (Losey and Vaughan, 2006). It accounts for an estimated 50-90% of the pest control occurring in crop fields, and may represent a sustainable and effective alternative to the use of chemical pesticides (Pimentel, 2005). The presence of natural enemies in and around fields is a prerequisite for such control. In agricultural landscapes, natural enemies benefit from high amounts of natural or seminatural habitat (Bianchi et al., 2006; Chaplin-Kramer et al., 2011), and from low-intensity farming practices such as organic farming (Bengtsson et al., 2005). However, little is known of how separate landscape factors such as habitat amount, landscape configuration and landscape diversity influence different natural enemies, or how they interact with local land use intensity (Batáry et al., 2011; Winqvist et al., 2012). In addition, few studies have tested whether increasing enemy diversity leads to a concomitant increase in pest control itself (Chaplin-Kramer et al., 2011). Disentangling these factors and their functional consequences for multiple taxa and spatial scales is necessary before landscapes can be actively and effectively managed for improved enemy diversity and pest control.

Landscape structure and local management intensity are important factors that influence natural enemy diversity. In locally extensive systems such as organic farming, most organisms are more abundant and species-rich than in locally intensive systems (Bengtsson et al., 2005; Batáry et al., 2011). However, to date, few studies have tested the presence of an interaction between local and landscape factors for enemy diversity, and none have done so across multiple spatial scales (Winqvist et al., 2012). Organic management is predicted to be most beneficial to enemy diversity in relatively simple landscapes, compared to i) cleared landscapes, where the species pool is insufficient to benefit from these measures, and ii) complex landscapes, where strong spillover from nearby habitats may override effects of local practices (Concepción et al., 2012; Tscharntke et al., 2012).

At the landscape scale, many organisms benefit from high levels of compositional complexity or heterogeneity, provided by natural or seminatural habitats near and around fields (Chaplin-Kramer et al., 2011; Fahrig et al., 2011). However, characterization of landscapes varies between studies and few efforts are made to provide a more general understanding of how different components of landscape structure affect enemy diversity across scales (Fahrig et al., 2011). Most studies define landscape complexity as the proportion of natural or seminatural habitat in a given radius around fields (landscape composition), and show that increasing amounts of natural or seminatural habitat increase the abundance and species richness of organisms that depend on such habitats (Steffan-Dewenter et al. 2002; Batáry et al., 2011; Chaplin-Kramer et al., 2011; Fahrig et al., 2011; Concepción et al., 2012). However, this parameter is frequently highly correlated with other variables, including patch shape complexity (‘configurational complexity’ or landscape configuration), and the diversity of land use types around fields (‘compositional complexity’ or landscape diversity) (Fahrig et al. 2011). In the few studies that do distinguish these factors, tests are restricted to one or two spatial scales of the landscape (Schweiger et al., 2005; Hendrickx et al., 2007; Billeter et al., 2008; Concepción et al., 2008; Bailey et al., 2010; Holzschuh et al., 2010), and/or applied only to a small number of taxa (Perović et al., 2010). These restrictions preclude the detection of tradeoffs between functional groups with varying body size, dispersal and other life history traits which may exhibit contrasting responses to changes in landscape structure across multiple scales (Bianchi et al. 2006; Schmidt et al., 2008). The prediction that for a fixed amount of natural or seminatural habitat, natural enemy diversity increases with increasing landscape diversity and configurational complexity, due to complementation and spillover between neighboring land cover types, remains virtually untested (Benton et al., 2003; Fahrig et al., 2011). Disentangling the separate effects of habitat amount, compositional and configurational complexity has important implications for cost-effective landscape management. If biodiversity and services benefit more from fine-grained landscapes and/or higher crop and habitat diversity, the economic costs, management implications and necessary incentives are different from those involving the conversion of productive areas to non-productive ones (Fahrig et al., 2011). In addition, because effects of landscape structure on organisms may occur at several scales simultaneously (Steffan-Dewenter et al., 2002; Rusch et al., 2011), disentangling these effects across multiple scales within the landscape itself is essential (Gabriel et al., 2010). To date, however, the effects of scale remain poorly understood (Tscharntke et al., 2012). In addition to increasing the certainty of results if obtained at more than one scale, tests at multiple scales may contribute considerably to accurately managing enemy diversity in these landscapes (Rusch et al., 2011). However, autocorrelation among spatial scales and limitations of available statistical tools currently constrain the analysis of landscape data at multiple spatial scales (Dormann & Seppele 2007, Tscharntke et al. 2012).

In this study, we aim to fill these gaps by investigating for seven different natural enemy taxa 1) the separate effects of landscape composition, configuration and diversity on natural enemy abundance and species richness; 2) the interactions between local and landscape factors; 3) the effects of spatial scale of the landscape; and 4) the links between enemy diversity, crop damage and crop biomass. We hypothesize i) that responses vary between groups of natural enemies; ii) that most predictive scales depend on the dispersal traits of organisms (Tscharntke et al., 2012); iii) that effects of landscape composition and diversity are more important than those of configuration; iv) that crop damage decreases and biomass increases with the abundance and richness of natural enemies.

4.2. Methods

4.2.1. Study area and sites

Sampling was performed from June to September 2009 in 35 crop fields of the Haean catchment, South Korea (long. 128°5’ to 128°11’E, lat. 38°13’ to 38°20’N; Figure S4.1). Fields were planted with one of five locally major annual crops (soy bean, potato, daikon radish, cabbage or irrigated rice; Table S4.1). Mean distance between fields of the same crop was 3±0.8 km (mean±sd), with a minimum of 500 m except two fields distant by 95.2 m. Fields were selected to vary both in local management intensity and along a gradient in landscape complexity (Table S4.1). Local management intensity compared conventional (n=19 fields) vs. “environmentally friendly” (hereafter organic; n=16 fields) inputs of fertilizer and pesticides. Other parameters of local intensity were uncorrelated with management (weed cover, height of field edges; Table S4.2) or were homogeneous across sites (all dry fields tilled, mulched monocultures with annual to bi-annual rotations; rice fields irrigated without rotation).

4.2.2. Natural enemy sampling, herbivory and biomass

Flying insect enemies. Predatory wasps, parasitoids, and syrphid flies were sampled in all sites using UV-coloured pan traps filled with water and a small amount of surfactant. Pan traps were set up in clusters of three traps (one yellow, one white and one blue) at crop height. Height of the traps was increased during the season as the crop grew.

Three pan trap clusters were placed in each field on a gradient of distance from the field edge (1 m, 10 m and 20 m), hereafter the “proximal” edge. Sampling was performed in clear weather by exposing pan traps for 24 hrs. Collected insects were placed in 82% ethanol in airtight Whirl-Paks© before identification. An average of 5.8 sampling rounds (range 3-7) was performed in each field throughout the season (Table S4.1). During each round, all sites were sampled within maximum 5 days. As crop phenologies differed throughout the season with potato and radish harvested earlier than other crops, the frequency of sampling was adjusted per crop type in order to include all phenological stages of each crop. Potato and radish fields were sampled at ~1 week intervals from June to August. Rice, cabbage and bean were sampled at ~1.5-2 week intervals from June to September. In analyses, temporal rounds represent the date of sampling and account for seasonal effects independently of phenological stages. Predatory wasps and syrphids were identified to species or morphospecies, and parasitoids to family (Appendix 4.1).

Ground-dwelling enemies. Spiders, carabid and staphylinid beetles were sampled using funnel (pitfall) traps in a subset of sites (n=30; Table S4.1). In dry fields, they were sampled using 5 traps placed on a gradient of distance from the proximal field edge (1 m, 5 m, 10 m, 15 m, 20 m). In irrigated rice fields, traps could not be placed inside the field and were installed along the proximal edge at 5 m-intervals. The traps consisted of a 12 cm-diameter plastic powder funnel, the wider rim of which was carefully placed at ground level. The narrow end of the funnel was concealed in a protective tube dug 30 cm into the ground. Freezing bags containing 1:3 ethylene glycol and water were attached to the narrow end of the funnel and served as receptacle for insects falling into the trap. Traps were protected from rainfall by a plastic roof positioned 3 cm above the funnel entrance. Funnel traps were activated on average for two periods of 10 days (range 1-3 periods; Table S4.1). Insects trapped after each period were rinsed and placed in airtight Whirl-Paks© with 82% ethanol before identification. Carabid and staphylinid beetles were identified to species or morphospecies (Appendix 4.1). Spiders were counted for total abundance.

Birds. Birds were sampled by point counts in a subset of sites (n=18; Table S4.1) by a team of 4 collectively trained observers. Counts were performed on average 2.7 times per site (range 1-5; Table S4.1), in clear weather between 6 and 10 am, during maximum daily bird activity. They recorded species, number of individuals and habitat occupied.

Crop herbivory and biomass. In order to relate natural enemy distribution to crop damage and yields, herbivory rates and crop biomass were measured in a subset of dry fields (n=23 and 26 for herbivory and biomass, respectively; Table S4.1). Herbivory was estimated after the rainy season in August using twelve 4 m² quadrats per field placed in a perpendicular cross at 1 m, 10 m and 20 m into the field from each edge. In one field, only 8 quadrats were used (1 m and 10 m) due to small size of the field. In each quadrat, the same number of leaves per crop was randomly collected (potato: 20 leaves, radish: 10, bean: 15). Leaves were scanned and herbivory was measured digitally with Adobe Photoshop CS3 to estimate the ratio of removed to total leaf area. At the end of the growing season, two crop plants were collected from three 1 m² quadrats surrounding pan trap locations at 1 m, 10 m, and 20 m from the proximal edge. Plants were weighed for total fresh biomass and fresh biomass of sellable parts.

4.2.3. Landscape structure

A polygon map of the Haean catchment based on Landsat imagery, regional land use maps and extensive ground-truthing in 2009, was used to calculate landscape parameters in ArcGIS 9.3 and R Statistical Software v. 2.15.1 (R Development Core Team, 2011). The land use category “forest” included deciduous forests surrounding the catchment (Figure S4.1), large forest patches (>0.5ha) and tall gallery forests in the central agricultural area. The category “seminatural” included seminatural field margins, intermediate regrowth and shrubby areas, forest edges (2 m wide buffers around the outside edge), and 1- and 2-year-old fallows.

Landscape parameters were calculated at 10 spatial scales from 100 to 1000 m radii around fields (100 m intervals). Parameters included 1) landscape composition, defined as the percent seminatural habitat around each plot (percent seminatural habitat, PSH) ; 2) landscape diversity, defined as Shannon´s index of habitat diversity (SHDI); 3) landscape configuration, defined as the ratio of mean patch perimeter to mean patch area (perimeter-area ratio, PAR). Landscape parameters did not correlate either with each other or with local crop and intensity variables (Spearman rank correlations $|\rho|<0.5$ at all scales; Table S4.2).

In all landscape analyses, heterogeneity of production cover types was not distinguished from that of (semi)natural cover types (Fahrig et al., 2011), as overall landscape heterogeneity depends on the combination of these factors, and increasing the diversity or shape complexity of production covers would inevitably lead to increased heterogeneity overall.

4.2.4. Statistical analyses

Focal taxa were restricted in the analysis to species and families acting as either predators or parasitoids of other insects (Table 4.1). Responses of natural enemy groups to local and landscape factors were analyzed using linear mixed effects models in package lme4 (Bates et al., 2012) with R Statistical Software v. 2.15.1 (R Development Core Team, 2011). The abundance and species richness of enemies was calculated as the total number of individuals and species found in each plot and sampling round (n=204 for pan traps, n=57 for pitfall traps, n=49 for point counts; Table S4.1). They were log(x+1)-transformed to improve conformance with assumptions of normality and homoscedasticity of model residuals. Full models included the fixed effects ‘crop type’ (bean, cabbage, potato, radish or rice) and ‘management’ (organic or conventional) as local explanatory variables; ‘composition’ (percent seminatural habitat, PSH), ‘configuration’ (perimeter-area ratio, PAR) and ‘diversity’ (Shannon´s habitat diversity index, SHDI) as landscape explanatory variables; and interactions between ‘management’ and landscape ‘composition’, ‘configuration’ and ‘diversity’, respectively. Landscape variables were centered and scaled prior to analysis using means and standard deviations of all plots and spatial scales (Table S4.1). Crossed random effects ‘plot’ and ‘temporal round’ were included to account for multiple sampling within plots and rounds.

Model selection based on Akaike´s Information Criterion (AICc) was performed on full models at each scale from 100 to 1000 m radii around fields (100m intervals), using the function dredge() in R package MuMIn (Barton, 2012). Subsets of best models with ΔAIC<2 were selected at each scale and are presented for each response variable in Table S4.3. AIC weights were calculated for selected models 1) within scales, representing the relative likelihood of models at the same scale; 2) across scales, representing the relative likelihood of all models at all scales. A measure of the importance of each explanatory variable was defined across scales as the sum of AIC weights across scales, of models containing the variable. It represents the probability that a variable is present in best models at all scales (and thus independently of scale choice).

‘Most predictive scales’ were defined for each enemy taxon as those with highest AIC weight of final best models for abundance. For each taxon, the most predictive scale for abundance was arbitrarily used for species richness as well. To ease interpretation, best models (ΔAIC=0) at most predictive scales were used to visualize results (Table S4.3).

Herbivory and biomass were analyzed as a function of the mean abundance and richness of natural enemy groups per plot, using separate linear regressions and an arcsine-square root-transformation for herbivory (Crawley, 2007), after visual inspection of residuals for violation of assumptions of normality and homoscedasticity.

4.3. Results

A total of 6303 individuals were sampled across 7 focal taxa (Table 4.1). They included 195 species and morphospecies and 27 parasitoid wasp families. Of these, 94% (209 species & parasitoid families) were categorized as antagonists of insects with the potential to contribute to pest and natural enemy interactions, and were included in the following analyses.

Effects of crop type and local management intensity

The diversity of focal taxa was affected variably by crop type (Figure 4.1). Mainly ground-dwellers (carabids, staphylinids and spiders) contributed to lower overall abundance and species richness of organisms in radish fields compared to other crops (F = 4.8, p = 0.004 and F = 4.1, p = 0.009 for abundance and species richness, respectively; Figures S4.2, S4.3).

Effects of local management intensity likewise differed between groups. Direct effects of local management were significant for syrphid flies and parasitoids, and less strong for predatory wasps (Figures 4.1, 4.2). On average, organic management led to 65% higher abundance of syrphids, 25% higher abundance of parasitoids and 32% higher family richness of parasitoids than conventional management (Figure 4.2).

Table 4.1. Species richness and abundance of organisms sampled in Haean, South Korea.

Taxonomic group	Function	Response	Total	Organic	Conventional	Identification
Syrphid flies	Pollinators and predators	S	21	21	14	Species
Diptera:Syrphidae		N	734	438	296	
	Predators only*	S	9	9	5	Species
		N	646	388	258	
Parasitoid wasps	Insect and plant parasitoids	S	27	25	24	Family
Hymenoptera:Parasitica		N	1217	657	560	
	Insect parasitoids only*	S	26	24	23	Family
		N	1215	656	559	
Predatory wasps	Predators & insect parasitoids	S	31	20	23	Species
Hymenoptera:Aculeata		N	218	110	108	
Carabid beetles	Predators	S	58	45	50	Species
Coleoptera:Carabidae		N	1255	507	748	
Staphylinid beetles	Predators	S	45	29	38	Species
Coleoptera:Staphylinidae		N	359	101	258	
Spiders	Predators	S	>1	>1	>1	Order
Araneae		N	1868	1044	824	
Birds	Predators	S	40	32	27	Species
Vertebrata:Aves		N	652	310	342	
All groups	All functions	S	222	172	176	Species/Family
		N	6303	3167	3136	
	Natural enemies*	S	209	159	166	Species/Family
		N	6213	3116	3097	

S: species richness, N: abundance.

'*' species acting as antagonists to insects (see Appendix 4.1).

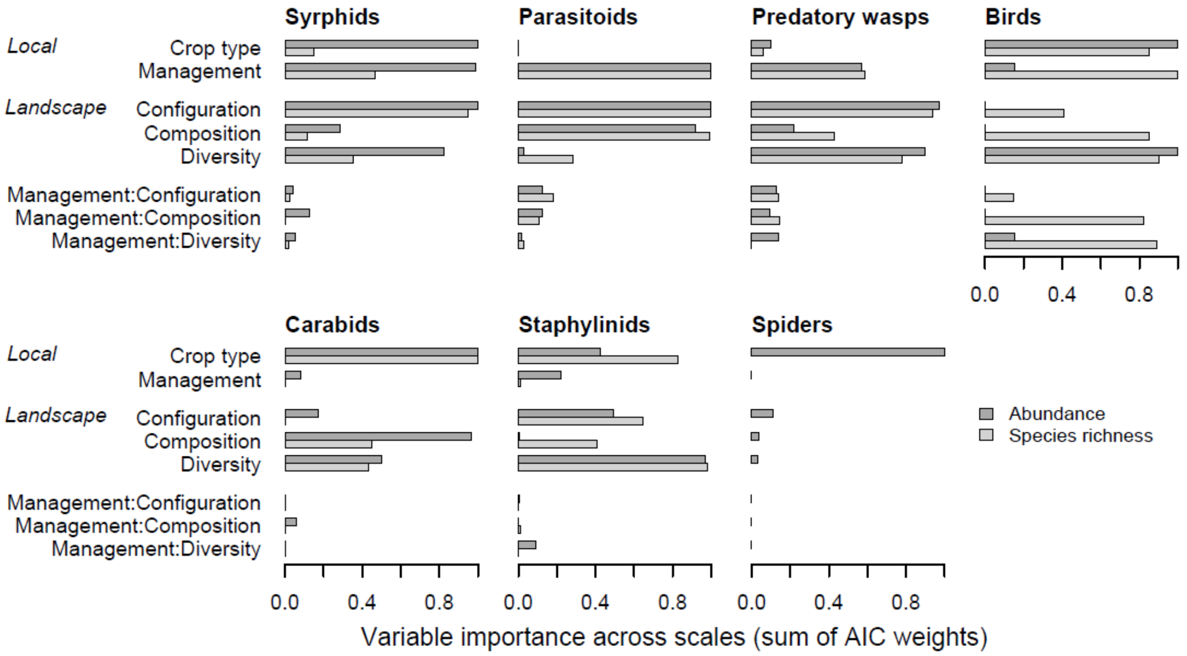

Figure 4.1. Importance of local and landscape variables for natural enemy abundance and species richness across scales. The importance (or weight) of a variable across scales is the sum of AIC weights of all models selecting it and represents the probability that a variable explains the response at any scale. It is calculated for the subsets of best models (ΔAIC<2) at all scales from 100m to 1000m radius around fields (100m intervals; Table S4.2). Local explanatory variables are crop type (potato, bean, radish, rice or cabbage) and management (organic or conventional). Landscape explanatory variables are configuration (perimeter-area ratio PAR), composition (percent seminatural habitat PSH) and diversity (Shannon´s habitat diversity index SHDI). Interactions are tested between local management and landscape configuration, composition and diversity, respectively.

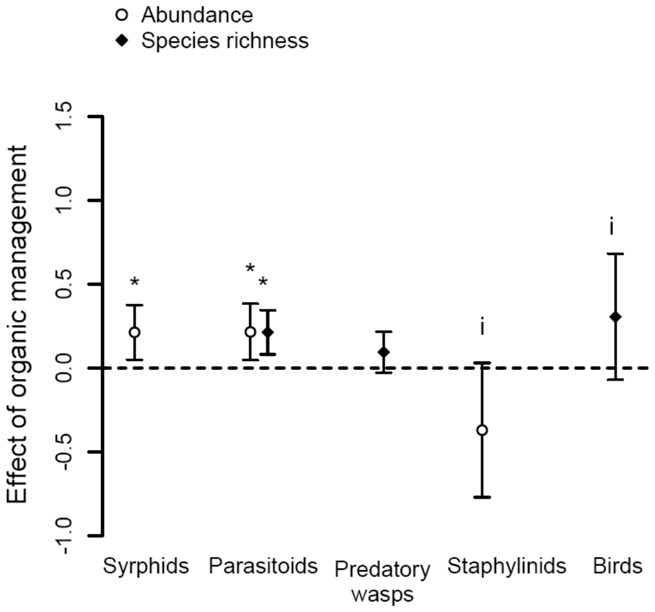

Figure 4.2. Effects of local management intensity on abundance and species richness of natural enemies. Values are final model estimates ± 95% CI of the effects of organic compared to conventional management. ‘*’ denotes significance of ‘management intensity’ in best AIC models at most predictive scales. ‘i’ denotes a significant interaction between management and landscape context. No effects of management were found for carabids or spiders (Table S4.2).

Effects of landscape configuration, composition and diversity across scales

Landscape configuration, composition and diversity had different and partly contrasting impacts on the abundance and species richness of natural enemy groups across scales (Figures 4.1, 4.3, S4.4-S4.6; Table S4.3). In addition, the most predictive spatial scale of the three landscape metrics tended to differ systematically among functional groups (Figure 4.3, Table S4.3). It was smaller for parasitoids and beetles (400 m), but larger for syrphids, wasps and birds (800-900 m). Across all tested scales, the slope (or strength of effects) of enemy responses to landscape metrics also increased with scale. Positive effects of landscape configuration were maintained across several scales for flying insects (syrphids, parasitoids and predatory wasps), staphylinids and birds, but not carabid beetles (Figures 4.3, 4.4, S4.4). Conversely, landscape composition positively influenced carabid beetle abundance at all scales and predatory wasp richness at small scales, but had either negative (parasitoids) or no impact on other groups (Figures 4.3, 4.4, S4.5). Particularly at large spatial scales (>700m), landscape habitat diversity had either positive (syrphids and birds) or negative effects on natural enemy groups (Figures 4.3, 4.4, S4.6). In contrast to other taxa, spiders were not affected by landscape parameters at any scale (Figures 4.3, S4.4-S4.6).

Interactions between local and landscape factors

Significant interactions between landscape context and local management were found at small scales (100-200m) for parasitoids and predatory wasps, and at 400 m for staphylinids (Figure 4.3). However, interactions were stable across multiple scales only in the case of birds (Figure 4.3). Bird species richness increased more strongly with landscape configuration and habitat diversity, respectively, in conventional compared to organic fields (Figures 4.4, S4.4, S4.6).

Effects on herbivory and biomass

Crop herbivory was positively related to the abundance and species richness of natural enemies (overall abundance $F=10.5$, $p=0.001$; overall richness $F=10.1$, $p=0.002$; Figure S4.7), particularly ground-dwellers (carabids, staphylinids and spiders; abundance $F=15.3$, $p<0.001$; richness $F=25.2$, $p<0.001$) and flying insects (syrphids, parasitoids and predatory wasps; abundance $F=6.8$, $p=0.01$; but not richness $F=2$, $p=0.2$). Crop biomass, however, was not significantly related either to natural enemy abundance or species richness, or to crop herbivory ($p>0.05$).

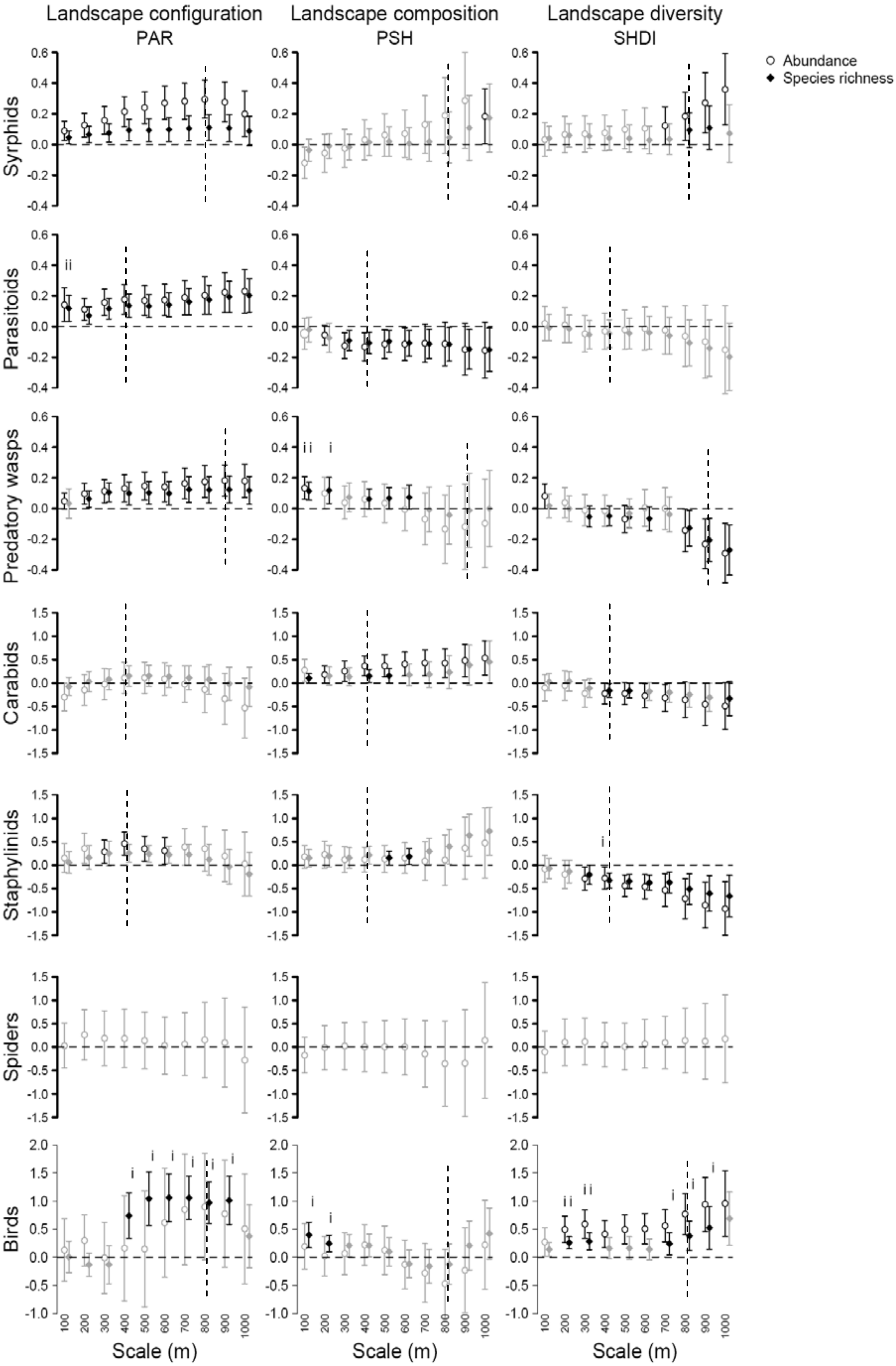

Figure 4.3. Effects of landscape configuration (perimeter-area ratio PAR), composition (percent seminatural habitat PSH) and diversity (Shannon´s habitat diversity index SHDI) on natural enemies at multiple spatial scales. Landscape variables are centered

and scaled (see Methods). Points are slope estimates of the lowest AIC linear mixed-effects model at each scale. Error bars represent 95% confidence intervals (CI). Effects not selected in final models are shown in grey (initial full model estimates ± 95% CI). ‘i’ indicates significant management:landscape interactions (estimates are shown for conventional management). Dashed lines indicate the most predictive scale for each enemy group. White circles: abundance, black squares: species richness.

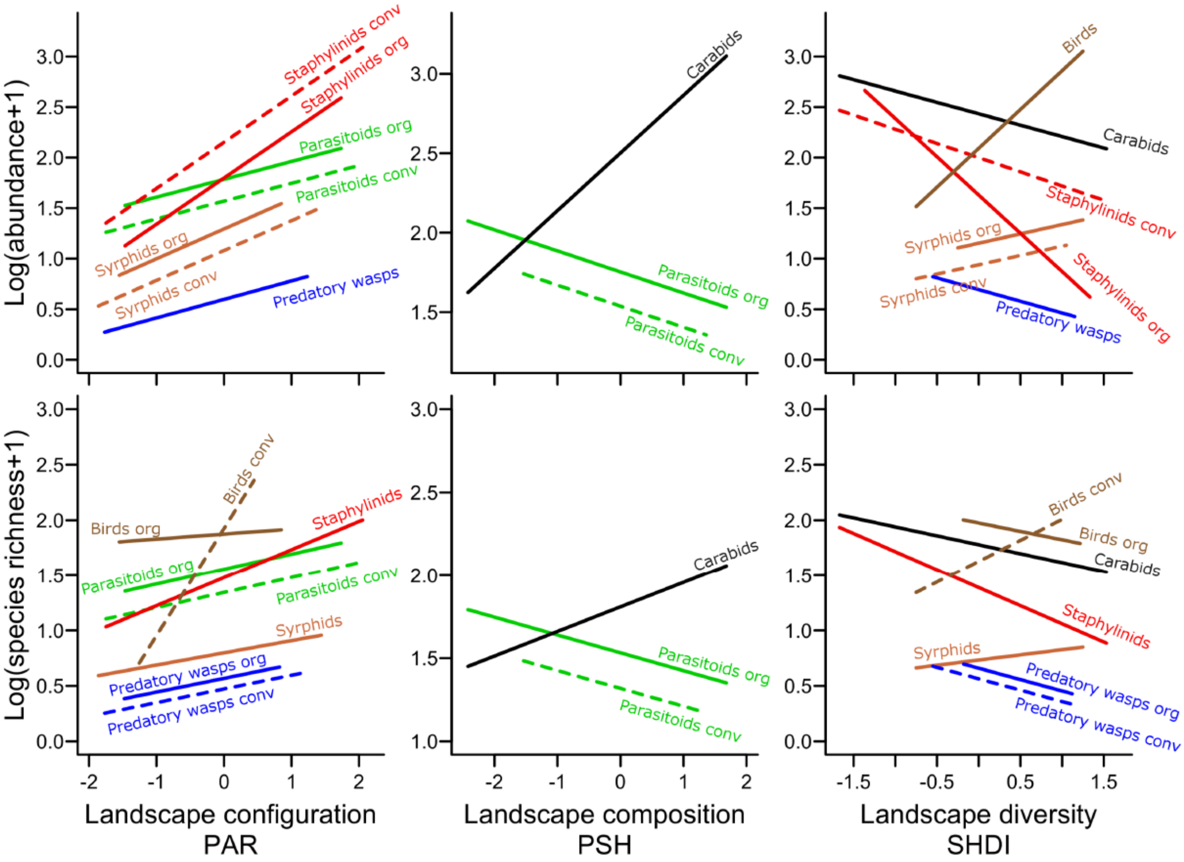

Figure 4.4. Combined effects of landscape configuration, composition and diversity on the abundance and species richness of multiple natural enemy groups. Predicted values of lowest AIC models are shown for each group at the most predictive scale (Table S4.2; regressions per group are shown in Figures S4.4-S4.6). Scales are 400 m (parasitoids, carabids and staphylinids), 800 m (syrphids and birds) and 900 m around fields (predatory wasps). Effects not selected in final models are not shown (spiders). Solid lines: organic, dashed lines: conventional management of fields.

4.4. Discussion

Landscape effects depend on scale

In this study, differential effects of landscape parameters and local and landscape interactions on natural enemies were observed at multiple spatial scales around crop fields. Both the presence and the intensity of landscape effects varied according to scale. When significant, effects of landscape configuration and composition were mainly present at all tested scales (syrphids, parasitoids, predatory wasps and carabids). In contrast, effects of landscape diversity, particularly on syrphids and predatory wasps, were restricted to scales above 700 m. The relative importance of different landscape parameters for enemy abundance and richness was thus scale-dependent (Rusch et al., 2011), which highlights the importance of analyzing several scales per organism. Although one-scale approaches (either arbitrary or ‘most predictive’) dominate the literature (Dormann and Seppelt, 2007), taking into account the simultaneous effects of landscape at multiple scales is essential for the applicability of landscape-wide management measures and the mechanistic understanding of landscape processes (Fahrig et al., 2011). Here, increases in habitat amount and configurational complexity are shown to impact most organism groups at both small and larger scales. In contrast, an increase in habitat diversity would impact syrphids and wasps only at large scales; and for all parameters, the larger the scale, the stronger the effects. Because of such scale-dependence, assessing the overall importance of landscape variables – in other words, finding out what matters – requires a method that integrates species responses across scales, even while it recognizes the scale-dependence of individual effects. Summing the weight of variables across all scales assesses landscape factors independently of arbitrary or less arbitrary scale choice, and incorporates their frequency (or overall relevance) across scales (Figure 4.1). A corollary is that variables found at only one or a few scales are given low overall importance. Indeed, as successive scales are necessarily correlated (Zuur et al., 2009), an effect occurring at only one scale has a higher probability of being a chance event, and confidence in its robustness is lower. This is reflected in our results by low probabilities of interactions between landscape and local management factors for several groups (≤ 0.1; Figure 4.1) when such interactions are present at only one scale (Figure 4.1).

When a most predictive scale was selected, this scale differed between enemy groups, in line with the idea that most important response scales are driven by the dispersal abilities of organisms (Rusch et al., 2011; Tscharntke et al., 2012). Ground-dwelling carabid and staphylinid beetles responded most to small scales (ca. 400 m) and may exhibit lower mobility than aerial species. Among aerial species, the mobile syrphids, predatory wasps and birds experienced the landscape at larger spatial scales (800-900 m). However, parasitoids, whose body size is frequently 10-15 times smaller than that of syrphids and predatory wasps, were more restricted in spatial scale (ca. 400 m), presumably because body size and dispersal distance tend to be positively correlated (Ritchie and Olff, 1999).

Local effects and interactions with landscape

Local, positive effects of organic compared to conventional management were found for syrphids, parasitoids and less strongly for predatory wasps, but not for ground-dwelling enemies which were influenced by crop type instead. Overall, ground-dwellers may have responded more to in-field complexity (weeds) and the degree of soil disturbance than to differences in agricultural inputs. Previous studies generally find positive effects of organic compared to conventional management (Bengtsson et al., 2005). However, in many studies, organic management is associated with higher weed cover, weed richness and lower disturbance levels (Batáry et al., 2011). Here, soil disturbance and vegetation complexity were uncorrelated with management (Table S4.2), thus management effects refer to the impact of conventional vs. organic fertilizer and pesticides use. In South Korea, effects of organic farming may be weak due to less strenuous regulations and to the recent character of conversions (<5 years), which particularly impacts beetles and spiders (Birkhofer et al., 2008) in contrast to flying insects, which are less strongly associated with long-term soil processes and may thus respond faster to local management changes.

Birds were the only group of natural enemies with stable interactions between landscape and local factors at multiple scales, in contrast to staphylinids (interaction at 400 m only). In the few available previous studies, out of several taxa, birds are also among the few to present such an interaction (Concepción et al., 2008). Similarly to Concepción et al. (2008), the patterns observed here for bird species richness are in line with current hypotheses (Tscharntke et al., 2012): in landscapes with low diversity and simple configuration, bird richness was higher in organic than conventional fields, but these differences were tempered in landscapes with high diversity or configurational complexity.

Differential effects of landscape configuration, composition and diversity

All natural enemy groups except spiders were affected by one or several landscape parameters within the scales of study. As spiders frequently disperse using wind and effects have been found for this group at scales up to 3 km around fields (Schmidt et al., 2008), it is possible that landscape effects on spiders occurred at larger scales than investigated here.

Excepting spiders and carabid beetles on which it had no effect, landscape configurational complexity had only positive impacts on enemy abundance and/or richness. This result underlines the importance of fine-grained landscapes with abundant habitat-crop interfaces that increase the amount of spillover between seminatural habitats and crops, for enhancing natural enemy diversity and pest control services (Hendrickx et al., 2007; Holzschuh et al., 2010; Fahrig et al., 2011; Tscharntke et al., 2012). In contrast, and contrary to expectations, the amount of habitat affected only two enemy groups, and was positive only for carabid beetles. Although previous studies find positive effects of habitat amount on many groups, few are designed to disentangle effects of habitat amount and configuration (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Fahrig et al., 2011). The present results indicate that positive effects of the amount of habitat in other studies may frequently be due to correlated differences in landscape configuration. Landscape configuration was also a major driver in the only previous study examining these effects on wasps (Holzschuh et al., 2010), whereas it did not greatly affect bees in a recent meta-analysis (Kennedy et al., 2013).

Increasing amounts of seminatural habitat, as well as increasing diversity of land use types, led to contrasting effects on all natural enemies except spiders. With more seminatural habitat, the abundance and richness of carabids in crop fields increased, but the diversity of parasitoids decreased. Landscape diversity had positive effects on birds and syrphids, but negative effects on three other groups (carabids, staphylinids and predatory wasps). Positive effects of these parameters may be linked with higher resource availability (landscape composition) and the contiguous presence of patches with different resources, leading to complementation (landscape diversity) (Fahrig et al., 2011; Tscharntke et al., 2012). However, higher diversity of resources also signifies lower amounts of each, which may have negative effects on organisms that depend on a few specific resources (Duelli, 1997). Overall, landscape composition and diversity were not suitable factors for predicting total enemy diversity, as their effects were highly taxon-specific and responses were not explained by any clear-cut pattern between groups.

Functional implications of contrasting responses between natural enemies

The contrasting responses of natural enemy groups at the landscape scale imply that choices need to be made in terms of which groups should be optimized, and whether the objectives are conservation, pest control or other functions. If the goal is to increase natural pest control, knowledge of which enemies are the most effective at reducing pests is required. However, because natural enemies do not act independently of each other, knowledge of the interactions occurring between enemies and of their consequences for pest control is also a prerequisite (Martin et al., 2013). In an exclusion experiment in the same region, Martin et al. (2013) show that flying insects (parasitoids, syrphids and predatory wasps) have the strongest potential to reduce densities of pest caterpillars, especially in complex landscapes. However, they also show that flying insect effectiveness for control of lepidopteran pests is reduced in the presence of birds, in conditions of high landscape complexity. Further studies also show that flying insects are more effective at controlling aphid populations than generalist ground-dwellers, such as carabid and staphylinid beetles (Schmidt et al., 2003; Holland et al., 2012; Martin et al. submitted). To date, ground-dwellers and flying insects have been found to have overall complementary interactions for pest control independently of the landscape (Holland et al., 2012; Martin et al. submitted). Here, groups with the highest potential for effective pest control are thus parasitoids, syrphids and predatory wasps, which benefit most from high levels of configurational complexity. As this parameter did not affect bird abundance, negative interactions may be avoided by this measure. Contrasting effects of landscape diversity on predatory wasps and birds are in line with the hypothesized intraguild predation behavior of birds on wasps (Martin et al., 2013). However, although some of these wasps prey on beetles or spiders (Appendix 4.1), corresponding contrasting effects of landscape on these groups, indicative of negative interactions, were not found.

A negative relationship between natural enemy abundance or richness, and crop damage and biomass, the ultimate factors of interest for actual service provision, has rarely been documented (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). The absence of such a relationship in our study indicates that, while natural enemy abundance and species richness increased with pest abundance, required densities for efficient pest control were not reached. Further, pest control is also the result of interactions both among natural enemies, and between natural enemies and pests (Chaplin-Kramer et al., 2011; Martin et al., 2013; Rusch et al., 2013). In fact, the positive relationship found here between crop damage and enemy diversity is in agreement with previous results of Martin et al. (2013), showing concomitant increases in pest density and crop damage with increasing landscape complexity.

Conclusion

The management implications of these results are clear. They suggest that agrienvironmental schemes should focus more on configurational complexity in agricultural landscapes, as small, complex-shaped fields interspersed with seminatural margins in a fine-grained mosaic are more beneficial to a wide range of pest-controlling organisms, than the simple proportion of non-crop habitat. Thus, in contrast to general assumptions, our results suggest that conversion of agricultural land to natural or semi-natural habitat is not the most effective measure to enhance natural enemy diversity, as long as fields retain large, homogeneous shapes. However, configurational complexity relies on a minimum of natural or seminatural habitats that was not below 6.6% in our study region. When considering habitat amount or diversity, contrasting responses between groups need to be balanced out in light of specific management objectives, and of the effectiveness of each group for natural pest control and other functions. This study shows that properly defining landscape parameters according to the organism, and at multiple scales, is key to managing landscapes for biodiversity. Improving associated ecosystem services depends on our ability to disentangle landscape effects on multiple taxa simultaneously, because services result not from the abundance of separate species, but from the interactions between them, with important implications for agroecological intensification and the design of sustainable multifunctional landscapes.

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4.7. Supplementary Tables

Table S 4.1. Plot characteristics and replicates per sampling method. Values are means (standard deviation).

Plot description			**Local factors**						**Landscape factors (mean of scales)**			
Crop type	Management	N plots	Distance to closest plot (m)	Mean distance between plots (m)	Field size (ha)	Altitude (m a.s.l)	Edge Height (cm)	Weed cover (%)	Composition (% seminatural)	Diversity (SHDI)	Configuration (PAR)	Same surrounding crop (%)
All crops	Conventional	19	100.3	2784.7 (1655.8)	0.55 (0.50)	490 (56)	100.1 (52.5)	17.5 (14.0)	25.05 (6.45)	1.11 (0.2)	0.091 (0.02)	13.73 (15.03)
	Organic	16	57.7	2222.5 (1233.2)	0.36 (0.20)	488 (44)	131.2 (80.0)	16.4 (12.3)	29.4 (9.09)	1.11 (0.22)	0.1 (0.03)	14.75 (15.11)
	Total	35	57.7	2764.3 (1392.2)	0.47 (0.41)	489 (50)	113.9 (67.0)	17.0 (13.0)	26.84 (7.93)	1.11 (0.21)	0.095 (0.03)	14.15 (15.05)
Bean	Conventional	4	1090.5	1567.7 (599.5)	0.34 (0.19)	451 (26)	106.6 (56.9)	6.5 (1.3)	22.7 (5.99)	1.15 (0.22)	0.094 (0.02)	4.41 (3.66)
	Organic	4	1400	3213.1 (1527.8)	0.51 (0.09)	529 (82)	82.8 (23.6)	15.7 (19.6)	24.18 (11.33)	1.14 (0.2)	0.067 (0.01)	7.11 (6.17)
	Total	8	708.4	2588.4 (1220.6)	0.41 (0.17)	484 (66)	94.7 (42.3)	11.1 (13.8)	23.33 (8.66)	1.15 (0.21)	0.082 (0.02)	5.57 (5.05)
Radish	Conventional	4	1130.4	2184.1 (857.5)	0.39 (0.16)	477 (50)	118.5 (53.6)	5.9 (2.7)	25.19 (3.82)	1.1 (0.21)	0.085 (0.01)	9.04 (7.64)
	Organic	4	95.2	2378.4 (1729.7)	0.40 (0.27)	493 (17)	155.5 (13.6)	11.0 (7.6)	30.07 (4.89)	1.15 (0.25)	0.103 (0.04)	9.18 (7.63)
	Total	8	95.2	2595.1 (1239)	0.39 (0.20)	484 (38)	134.9 (43.5)	8.5 (5.9)	27.36 (4.95)	1.12 (0.23)	0.093 (0.03)	9.1 (7.6)
Potato	Conventional	4	2013.5	3553.5 (1467.1)	0.65 (0.32)	512 (62)	112.1 (24.9)	26.4 (10.4)	27.89 (8.88)	1.14 (0.19)	0.103 (0.03)	11.32 (7.75)
	Organic	4	499.4	2088.9 (1136)	0.32 (0.25)	467 (12)	228.0 (83.3)	22.3 (5.0)	33.51 (8.84)	1.14 (0.21)	0.119 (0.03)	9.39 (5.33)
	Total	8	499.4	2736.2 (1307.4)	0.51 (0.32)	492 (50)	170.0 (84.1)	24.4 (7.9)	30.3 (9.24)	1.14 (0.2)	0.11 (0.03)	10.5 (6.85)
Rice	Conventional	4	974.6	2447.3 (1378.9)	0.31 (0.17)	465 (41)	39.1 (33.1)	-	25.5 (6.19)	1.04 (0.2)	0.098 (0.02)	29.98 (21.75)
	Organic	4	1325.1	1840.2 (625.5)	0.23 (0.07)	467 (24)	58.5 (29.5)	-	29.55 (9.05)	1.03 (0.19)	0.109 (0.02)	30.06 (19.13)
	Total	8	974.6	2769.2 (1268.9)	0.27 (0.12)	466 (31)	48.8 (30.9)	-	27.53 (7.98)	1.04 (0.2)	0.104 (0.02)	30.02 (20.37)
Cabbage	Conventional	3	266.3	4473.1 (3645.6)	1.30 (0.98)	570 (9)	126.3 (57.4)	36.1 (0)	23.56 (5.68)	1.13 (0.13)	0.073 (0.02)	15.53 (13.41)
	Total	3	266.3	4473.1 (3645.6)	1.30 (0.98)	570 (9)	126.3 (57.4)	36.1 (0)	23.56 (5.68)	1.13 (0.13)	0.073 (0.02)	15.53 (13.41)

Table S 4.1 (continued)

Plot description			**Replicates per sampling method**										
Crop type	Management	N plots	Plots with pan trap sampling	Number of censuses (plots***censuses**)	N obs	Plots with pitfall trap sampling	Number of censuses (plots***censuses**)	N obs	Plots with bird point counts	Number of censuses (plots***censuses**)	N obs	N Herbivory	N Biomass
All crops	Conventional	19	19	13***6**+3***3**+**5**+2***7**	106	19	17***2**+**1**+1***3**	38	10	8***2**+**1**+**3**	20	11	15
	Organic	16	16	14***6**+2***7**	98	11	8***2**+3***1**	19	8	2***2**+2***3**+**4**+3***5**	29	12	11
	Total	35	35	27***6**+4***7**+**5**+3***3**	204	30	25***2**+4***1**+1***3**	57	18	**1**+10***2**+3***3**+**4**+3***5**	49	23	26
Bean	Conventional	4	4	2***6**+2***7**	26	4	3***2**+1***3**	9	3	3***2**	6	4	3
	Organic	4	4	2***6**+2***7**	26	4	4***2**	8	3	**2**+**3**+**4**	9	4	3
	Total	8	8	4***6**+4***7**	52	8	7***2**+1***3**	17	6	4***2**+**3**+**4**	15	8	6
Radish	Conventional	4	4	4***6**	24	4	3***2**+**1**	7	3	2***2**+**1**	5	4	3
	Organic	4	4	4***6**	24	2	2***1**	2	2	**5**+**3**	8	4	3
	Total	8	8	8***6**	48	6	3***2**+3***1**	9	5	2***2**+**1**+**5**+**3**	13	8	6
Potato	Conventional	4	4	4***6**	24	4	4***2**	8	1	**2**	2	2	3
	Organic	4	4	4***6**	24	1	1***1**	1	2	2***5**	10	4	2
	Total	8	8	8***6**	48	5	4***2**+**1**	9	3	2***5**+**2**	12	6	5
Rice	Conventional	4	4	3***6**+**5**	23	4	4***2**	8	3	2***2**+**3**	7	-	3
	Organic	4	4	4***6**	24	4	4***2**	8	1	**2**	2	-	3
	Total	8	8	7***6**+**5**	47	8	8***2**	16	4	3***2**+**3**	9	-	6
Cabbage	Conventional	3	3	3***3**	9	3	3***2**	6	-	-	-	1	3
	Total	3	3	3***3**	9	3	3***2**	6	-	-	-	1	3

Table S 4.2. Spearman correlation coefficients ρ between local, landscape and abiotic variables at each scale. Values |ρ|>0.5 are in bold. Correlations between variables included in models were |ρ| <0.5 at all scales (in frames). They include: crop type (Crop), management type (organic or conventional; Mgmt), landscape configuration (PAR), landscape composition (PSH) and landscape diversity (SHDI).

Variable name	Scale	Crop	Mgmt	Weed cover	Weed richness	Edge height	Altitude	PAR	PT	SHDI
Management type (Mgmt)	100 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.053	0.115	0.493	0.250	0.139	-0.019			
Landscape composition (PT)		0.011	0.144	0.359	-0.146	0.464	0.355	0.075		
Landscape diversity (SHDI)		-0.413	-0.260	-0.093	0.335	0.175	-0.088	-0.048	0.035	
% same surrounding crop (SSC)		**0.730**	-0.007	-0.158	-0.090	-0.189	-0.114	0.000	-0.069	-0.363
Management type (Mgmt)	200 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.110	0.188	**0.571**	0.269	0.186	-0.007			
Landscape composition (PT)		0.099	0.101	0.221	-0.246	0.497	0.312	0.288		
Landscape diversity (SHDI)		-0.227	0.051	0.187	**0.510**	0.079	0.029	0.054	-0.005	
% same surrounding crop (SSC)		**0.665**	0.036	0.068	-0.102	-0.071	0.005	0.196	0.204	-0.300
Management type (Mgmt)	300 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.109	0.123	**0.572**	0.214	0.161	-0.008			
Landscape composition (PT)		0.180	0.260	0.007	-0.258	0.489	0.397	0.327		
Landscape diversity (SHDI)		-0.147	0.014	0.193	0.415	0.111	0.059	0.326	-0.023	
% same surrounding crop (SSC)		**0.594**	0.072	0.154	-0.039	0.171	0.081	0.269	0.319	-0.260
Management type (Mgmt)	400 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.133	0.159	**0.539**	0.131	0.075	-0.048			
Landscape composition (PT)		0.235	0.245	-0.067	-0.175	0.300	0.479	0.302		
Landscape diversity (SHDI)		-0.199	0.087	0.138	**0.572**	0.246	0.128	0.307	0.097	
% same surrounding crop (SSC)		**0.503**	0.123	0.124	-0.046	0.189	0.151	0.082	0.209	-0.391
Management type (Mgmt)	500 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.201	0.217	**0.532**	0.129	-0.071	-0.091			
Landscape composition (PT)		0.251	0.303	-0.043	-0.178	0.229	**0.513**	0.277		
Landscape diversity (SHDI)		-0.248	0.173	0.002	0.483	0.286	0.216	0.170	0.081	
% same surrounding crop (SSC)		**0.510**	0.101	0.178	-0.054	0.079	0.171	0.180	0.302	-0.443

Variable name	Scale	Crop	Mgmt	Weed cover	Weed richness	Edge height	Altitude	PAR	PT	SHDI
Management type (Mgmt)	600 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.208	0.224	**0.537**	0.135	0.004	-0.069			
Landscape composition (PT)		0.238	0.419	-0.011	-0.175	0.346	**0.557**	0.297		
Landscape diversity (SHDI)		-0.303	0.274	0.004	0.480	0.396	0.249	0.131	0.194	
% same surrounding crop (SSC)		**0.518**	0.007	0.117	-0.064	0.039	0.139	0.296	0.256	-0.469
Management type (Mgmt)	700 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.216	0.260	0.465	0.036	-0.107	-0.120			
Landscape composition (PT)		0.121	0.447	0.179	-0.127	0.282	**0.604**	0.332		
Landscape diversity (SHDI)		-0.299	0.231	-0.127	0.439	0.371	0.204	0.064	0.130	
% same surrounding crop (SSC)		**0.552**	0.007	0.144	-0.076	0.082	0.104	0.315	0.206	-0.448
Management type (Mgmt)	800 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.236	0.267	0.446	-0.015	-0.107	-0.147			
Landscape composition (PT)		0.134	0.498	0.335	-0.180	0.275	**0.537**	0.445		
Landscape diversity (SHDI)		-0.328	0.137	-0.254	0.335	0.279	0.215	-0.035	-0.044	
% same surrounding crop (SSC)		**0.575**	0.101	0.235	0.016	0.050	0.068	0.373	0.268	-0.385
Management type (Mgmt)	900 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.262	0.245	0.434	-0.031	0.000	-0.214			
Landscape composition (PT)		0.169	0.476	0.307	-0.277	0.179	0.477	0.498		
Landscape diversity (SHDI)		-0.390	0.087	-0.213	0.266	0.225	0.220	-0.076	-0.137	
% same surrounding crop (SSC)		**0.588**	0.101	0.200	-0.036	0.071	0.068	0.371	0.301	-0.422
Management type (Mgmt)	1000 m	0.015								
Weed cover		0.000	0.187							
Weed richness		-0.033	0.043	0.357						
Edge height		-0.263	0.131	-0.088	-0.176					
Altitude		-0.196	0.311	-0.077	-0.061	0.421				
Landscape configuration (PAR)		0.236	0.144	0.353	-0.040	-0.079	-0.378			
Landscape composition (PT)		0.167	0.382	0.296	-0.317	0.118	0.407	0.406		
Landscape diversity (SHDI)		-0.381	0.087	-0.278	0.171	0.186	0.183	-0.165	-0.240	
% same surrounding crop (SSC)		**0.611**	0.101	0.237	-0.029	0.043	0.076	0.227	0.308	-0.477

Table S 4.3. Results of linear mixed effects models relating (log+1)-transformed natural enemy abundance and species richness to explanatory variables. Results are shown for all scales from 100m to 1000m radii around fields. Models with the lowest AIC at the corresponding scale are in bold. Arrows indicate best models at the most predictive scale. Slopes of continuous variables are noted (estimate±SE). Explanatory variables are: Crop (4 annual crop types); Mgmt (organic vs. conventional management); PAR (landscape configuration as perimeter-area ratio); PSH (landscape composition as percent seminatural habitat); SHDI (landscape diversity as Shannon´s habitat diversity index) and interactions. Natural enemies are a-b) syrphids, c-d) parasitoids, e-f) predatory wasps, g-h) carabid beetles, i-j) staphylinid beetles, k) spiders, l-m) insectivorous birds.

Response	Scale	Model									df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
a) Syrphid	**100**	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.09±0.03) PAR**						**10**	**-193.6**	**408.35**	**0**	**0.29**	0.01	0.00
abundance	100	Int.	+ Crop	+ Mgmt	+ (0.09±0.03) PAR	+ (-0.04±0.03) PSH					11	-192.69	408.75	0.4	0.24	0.01	0.00
	100	Int.	+ Crop	+ Mgmt	+ (0.16±0.06) PAR	+ (-0.06±0.03) PSH		+ Mgmt:PAR			12	-191.75	409.14	0.79	0.19	0.01	0.00
	100	Int.	+ Crop	+ Mgmt	+ (0.21±0.07) PAR	+ (-0.11±0.05) PSH		+ Mgmt:PAR	+ Mgmt:PSH		13	-190.83	409.58	1.23	0.16	0.01	0.00
	100	Int.	+ Crop	+ Mgmt	+ (0.13±0.06) PAR			+ Mgmt:PAR			11	-193.33	410.03	1.68	0.12	0.01	0.00
	200	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.13±0.04) PAR**						**10**	**-192.77**	**406.68**	**0**	**0.29**	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.13±0.04) PAR		+ (0.08±0.05) SHDI				11	-191.71	406.80	0.12	0.27	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.13±0.04) PAR	+ (-0.04±0.04) PSH					11	-192.14	407.66	0.98	0.18	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.13±0.04) PAR	+ (-0.04±0.04) PSH	+ (0.07±0.05) SHDI				12	-191.18	407.99	1.32	0.15	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.13±0.04) PAR		+ (0.06±0.06) SHDI			+ Mgmt:SHDI	12	-191.51	408.65	1.98	0.11	0.00	0.00
	300	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.16±0.05) PAR**						**10**	**-192.09**	**405.31**	**0**	**0.44**	0.00	0.00
	300	Int.	+ Crop	+ Mgmt	+ (0.14±0.05) PAR		+ (0.06±0.05) SHDI				11	-191.39	406.15	0.83	0.29	0.00	0.00
	300	Int.	+ Crop	+ Mgmt	+ (0.17±0.05) PAR	+ (-0.05±0.05) PSH					11	-191.5	406.38	1.06	0.26	0.00	0.00
	400	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.21±0.05) PAR**						**10**	**-189.7**	**400.54**	**0**	**0.7**	0.00	0.01
	400	Int.	+ Crop	+ Mgmt	+ (0.20±0.05) PAR		+ (0.03±0.05) SHDI				11	-189.41	402.20	1.66	0.3	0.00	0.00
	500	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.24±0.05) PAR**						**10**	**-188.44**	**398.02**	**0**	**0.52**	0.03	0.02
	500	Int.	+ Crop	+ Mgmt	+ (0.23±0.05) PAR		+ (0.04±0.05) SHDI				11	-188.1	399.58	1.55	0.24	0.03	0.01
	500	Int.	+ Crop	+ Mgmt	+ (0.26±0.06) PAR		+ (0.10±0.06) SHDI			+ Mgmt:SHDI	12	-186.98	399.59	1.57	0.24	0.03	0.01
	600	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.27±0.06) PAR**						**10**	**-187.13**	**395.41**	**0**	**0.45**	0.12	0.08
	600	Int.	+ Crop	+ Mgmt	+ (0.26±0.06) PAR		+ (0.08±0.06) SHDI				11	-186.18	395.74	0.33	0.38	0.12	0.07
	600	Int.	+ Crop	+ Mgmt	+ (0.28±0.06) PAR		+ (0.11±0.07) SHDI			+ Mgmt:SHDI	12	-185.82	397.28	1.88	0.17	0.12	0.03
	700	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.28±0.06) PAR**		**+ (0.12±0.06) SHDI**				**11**	**-185.54**	**394.46**	**0**	**0.54**	0.15	0.13
	700	Int.	+ Crop	+ Mgmt	+ (0.29±0.06) PAR						10	-187.41	395.96	1.51	0.25	0.15	0.06
	700	Int.	+ Crop	+ Mgmt	+ (0.28±0.06) PAR	+ (0.12±0.09) PSH	+ (0.12±0.06) SHDI		+ Mgmt:PSH		13	-184.21	396.33	1.87	0.21	0.15	0.05
➡	**800**	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.30±0.06) PAR**		**+ (0.18±0.08) SHDI**				**11**	**-185.29**	**393.96**	**0**	**0.73**	0.27	0.17
	800	Int.	+ Crop	+ Mgmt	+ (0.29±0.07) PAR	+ (0.04±0.07) PSH	+ (0.18±0.08) SHDI				12	-185.15	395.93	1.98	0.27	0.27	0.06
	900	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.28±0.07) PAR**		**+ (0.27±0.10) SHDI**				**11**	**-186.08**	**395.54**	**0**	**0.4**	0.20	0.08
	900	Int.	+ Crop	+ Mgmt	+ (0.25±0.07) PAR	+ (0.09±0.09) PSH	+ (0.27±0.10) SHDI				12	-185.55	396.73	1.19	0.22	0.20	0.04
	900	Int.	+ Crop	+ Mgmt	+ (0.24±0.07) PAR	+ (0.23±0.13) PSH	+ (0.27±0.10) SHDI		+ Mgmt:PSH		13	-184.45	396.81	1.27	0.21	0.20	0.04
	900	Int.	+ Crop	+ Mgmt	+ (0.32±0.10) PAR		+ (0.28±0.10) SHDI	+ Mgmt:PAR			12	-185.9	397.43	1.89	0.16	0.20	0.03
	1000	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.20±0.08) PAR**	**+ (0.18±0.09) PSH**	**+ (0.36±0.12) SHDI**				**12**	**-186.02**	**397.67**	**0**	**0.28**	0.23	0.03
	1000	Int.	+ Crop	+ Mgmt	+ (0.19±0.08) PAR	+ (0.31±0.13) PSH	+ (0.38±0.12) SHDI		+ Mgmt:PSH		13	-184.95	397.82	0.15	0.26	0.23	0.02
	1000	Int.	+ Crop	+ Mgmt	+ (0.20±0.08) PAR	+ (0.18±0.09) PSH	+ (0.30±0.14) SHDI			+ Mgmt:SHDI	13	-185.65	399.22	1.55	0.13	0.23	0.01
	1000	Int.	+ Crop	+ Mgmt	+ (0.26±0.07) PAR		+ (0.32±0.12) SHDI				11	-187.98	399.33	1.66	0.12	0.23	0.01
	1000	Int.	+ Crop	+ Mgmt	+ (0.08±0.15) PAR	+ (0.39±0.16) PSH	+ (0.38±0.12) SHDI	+ Mgmt:PAR	+ Mgmt:PSH		14	-184.63	399.48	1.81	0.11	0.23	0.01
	1000	Int.	+ Crop		+ (0.19±0.08) PAR	+ (0.26±0.09) PSH	+ (0.39±0.12) SHDI				11	-188.05	399.48	1.82	0.11	0.23	0.01

Response	Scale	Model							df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
b) Syrphid richness	**100**	**Int.**			**+ (0.04±0.02) PAR**				**5**	**-106.67**	**223.65**	**0**	**0.23**	0.07	0.01
	100	Int.		+ Mgmt	+ (0.04±0.02) PAR				6	-105.85	224.13	0.48	0.18	0.07	0.01
	100	Int.		+ Mgmt	+ (0.04±0.02) PAR	+ (-0.02±0.02) PSH			7	-105.02	224.61	0.96	0.14	0.07	0.01
	100	Int.			+ (0.05±0.02) PAR	+ (-0.02±0.02) PSH			6	-106.15	224.73	1.08	0.13	0.07	0.01
	100	Int.		+ Mgmt					5	-107.22	224.74	1.09	0.13	0.07	0.01
	100	Int.							4	-108.59	225.39	1.74	0.1	0.07	0.00
	100	Int.		+ Mgmt		+ (-0.02±0.02) PSH			6	-106.51	225.44	1.79	0.09	0.07	0.00
	200	**Int.**			**+ (0.06±0.03) PAR**				**5**	**-106.03**	**222.36**	**0**	**0.17**	0.01	0.02
	200	Int.		+ Mgmt	+ (0.06±0.03) PAR		+ (0.06±0.04) SHDI		7	-104.09	222.76	0.4	0.14	0.01	0.02
	200	Int.			+ (0.07±0.03) PAR		+ (0.05±0.04) SHDI		6	-105.17	222.77	0.41	0.14	0.01	0.02
	200	Int.		+ Mgmt	+ (0.06±0.03) PAR				6	-105.3	223.03	0.67	0.12	0.01	0.02
	200	Int.			+ (0.07±0.03) PAR	+ (-0.02±0.03) PSH			6	-105.62	223.66	1.3	0.09	0.01	0.01
	200	Int.	+ Crop	+ Mgmt	+ (0.07±0.03) PAR		+ (0.08±0.03) SHDI		11	-100.23	223.83	1.47	0.08	0.01	0.01
	200	Int.		+ Mgmt	+ (0.06±0.03) PAR	+ (-0.03±0.02) PSH	+ (0.05±0.03) SHDI		8	-103.55	223.84	1.48	0.08	0.01	0.01
	200	Int.		+ Mgmt	+ (0.06±0.03) PAR	+ (-0.03±0.02) PSH			7	-104.72	224.01	1.65	0.07	0.01	0.01
	200	Int.			+ (0.07±0.03) PAR	+ (-0.02±0.02) PSH	+ (0.05±0.04) SHDI		7	-104.81	224.19	1.83	0.07	0.01	0.01
	200	Int.	+ Crop		+ (0.08±0.03) PAR		+ (0.07±0.03) SHDI		10	-101.58	224.30	1.94	0.06	0.01	0.01
	300	**Int.**			**+ (0.08±0.03) PAR**				**5**	**-105.94**	**222.19**	**0**	**0.27**	0.04	0.02
	300	Int.		+ Mgmt	+ (0.07±0.03) PAR				6	-105.25	222.92	0.73	0.19	0.04	0.02
	300	Int.			+ (0.07±0.03) PAR		+ (0.04±0.04) SHDI		6	-105.36	223.15	0.95	0.17	0.04	0.01
	300	Int.		+ Mgmt	+ (0.06±0.03) PAR		+ (0.04±0.04) SHDI		7	-104.52	223.61	1.42	0.14	0.04	0.01
	300	Int.			+ (0.08±0.03) PAR	+ (-0.02±0.03) PSH			6	-105.67	223.76	1.57	0.13	0.04	0.01
	300	Int.		+ Mgmt	+ (0.08±0.03) PAR	+ (-0.03±0.03) PSH			7	-104.79	224.15	1.95	0.1	0.04	0.01
	400	**Int.**			**+ (0.09±0.04) PAR**				**5**	**-105.58**	**221.46**	**0**	**0.37**	0.06	0.03
	400	Int.		+ Mgmt	+ (0.08±0.04) PAR				6	-104.79	222.01	0.55	0.28	0.06	0.03
	400	Int.			+ (0.09±0.04) PAR		+ (0.03±0.03) SHDI		6	-105.26	222.95	1.49	0.18	0.06	0.02
	400	Int.	+ Crop		+ (0.13±0.04) PAR				9	-102.1	223.13	1.67	0.16	0.06	0.01
	500	**Int.**			**+ (0.09±0.04) PAR**				**5**	**-105.81**	**221.92**	**0**	**0.32**	0.11	0.03
	500	Int.		+ Mgmt	+ (0.08±0.04) PAR				6	-104.93	222.28	0.37	0.26	0.11	0.02
	500	Int.			+ (0.09±0.04) PAR		+ (0.03±0.04) SHDI		6	-105.46	223.35	1.43	0.15	0.11	0.01
	500	Int.	+ Crop		+ (0.13±0.04) PAR				9	-102.34	223.60	1.69	0.14	0.11	0.01
	500	Int.	+ Crop	+ Mgmt	+ (0.12±0.04) PAR				10	-101.3	223.74	1.82	0.13	0.11	0.01
	600	**Int.**			**+ (0.10±0.04) PAR**				**5**	**-105.78**	**221.86**	**0**	**0.2**	0.11	0.03
	600	Int.		+ Mgmt	+ (0.09±0.04) PAR				6	-104.76	221.96	0.09	0.19	0.11	0.03
	600	Int.			+ (0.09±0.04) PAR		+ (0.05±0.04) SHDI		6	-105.1	222.62	0.76	0.13	0.11	0.02
	600	Int.	+ Crop	+ Mgmt	+ (0.14±0.04) PAR				10	-100.8	222.75	0.88	0.13	0.11	0.02
	600	Int.	+ Crop		+ (0.14±0.04) PAR				9	-102.08	223.09	1.23	0.11	0.11	0.02
	600	Int.		+ Mgmt	+ (0.09±0.04) PAR		+ (0.04±0.04) SHDI		7	-104.34	223.25	1.39	0.1	0.11	0.01
	600	Int.		+ Mgmt	+ (0.06±0.06) PAR			+ Mgmt:PAR	7	-104.52	223.60	1.74	0.08	0.11	0.01
	600	Int.	+ Crop		+ (0.14±0.04) PAR		+ (0.05±0.04) SHDI		10	-101.33	223.80	1.94	0.07	0.11	0.01

	700	**Int.**			**+ (0.10±0.04) PAR**				**5**	**-105.81**	**221.93**	**0**	**0.17**	0.12	0.03
	700	Int.		+ Mgmt	+ (0.10±0.04) PAR				6	-104.76	221.94	0.01	0.17	0.12	0.03
	700	Int.			+ (0.10±0.04) PAR		+ (0.07±0.05) SHDI		6	-104.84	222.11	0.18	0.16	0.12	0.02
	700	Int.		+ Mgmt	+ (0.10±0.04) PAR		+ (0.05±0.05) SHDI		7	-104.09	222.75	0.82	0.12	0.12	0.02
	700	Int.	+ Crop	+ Mgmt	+ (0.14±0.04) PAR				10	-100.99	223.13	1.2	0.1	0.12	0.01
	700	Int.	+ Crop		+ (0.15±0.04) PAR		+ (0.07±0.04) SHDI		10	-101.25	223.64	1.71	0.07	0.12	0.01
	700	Int.	+ Crop		+ (0.15±0.04) PAR				9	-102.37	223.66	1.73	0.07	0.12	0.01
	700	Int.		+ Mgmt	+ (0.07±0.06) PAR			+ Mgmt:PAR	7	-104.63	223.82	1.89	0.07	0.12	0.01
	700	Int.	+ Crop	+ Mgmt	+ (0.14±0.04) PAR		+ (0.05±0.04) SHDI		11	-100.25	223.88	1.95	0.07	0.12	0.01
➡	**800**	**Int.**			**+ (0.11±0.04) PAR**		**+ (0.09±0.06) SHDI**		**6**	**-104.73**	**221.88**	**0**	**0.26**	0.18	0.03
	800	Int.			+ (0.11±0.05) PAR				5	-105.95	222.19	0.31	0.22	0.18	0.02
	800	Int.		+ Mgmt	+ (0.10±0.04) PAR				6	-104.89	222.20	0.32	0.22	0.18	0.02
	800	Int.		+ Mgmt	+ (0.10±0.04) PAR		+ (0.08±0.06) SHDI		7	-103.97	222.51	0.63	0.19	0.18	0.02
	800	Int.		+ Mgmt	+ (0.10±0.04) PAR		+ (0.04±0.07) SHDI	+ Mgmt:SHDI	8	-103.55	223.84	1.96	0.1	0.18	0.01
	900	**Int.**			**+ (0.11±0.05) PAR**		**+ (0.11±0.07) SHDI**		**6**	**-105.26**	**222.95**	**0**	**0.18**	0.15	0.02
	900	Int.			+ (0.10±0.05) PAR				5	-106.34	222.98	0.04	0.18	0.15	0.02
	900	Int.		+ Mgmt	+ (0.09±0.05) PAR				6	-105.28	222.98	0.04	0.18	0.15	0.02
	900	Int.		+ Mgmt	+ (0.10±0.04) PAR		+ (0.1±0.07) SHDI		7	-104.38	223.34	0.39	0.15	0.15	0.01
	900	Int.		+ Mgmt	+ (0.10±0.04) PAR		+ (0.05±0.09) SHDI	+ Mgmt:SHDI	8	-103.93	224.61	1.66	0.08	0.15	0.01
	900	Int.		+ Mgmt					5	-107.22	224.74	1.79	0.08	0.15	0.01
	900	Int.			+ (0.09±0.05) PAR	+ (0.03±0.06) PSH	+ (0.11±0.07) SHDI		7	-105.11	224.79	1.85	0.07	0.15	0.01
	900	Int.			+ (0.09±0.05) PAR	+ (0.03±0.06) PSH			6	-106.19	224.80	1.86	0.07	0.15	0.01
	1000	**Int.**		**+ Mgmt**	**+ (0.09±0.05) PAR**				**6**	**-105.73**	**223.88**	**0**	**0.15**	0.15	0.01
	1000	Int.			+ (0.10±0.05) PAR				5	-106.85	224.00	0.12	0.14	0.15	0.01
	1000	Int.				+ (0.11±0.06) PSH			5	-107.18	224.66	0.78	0.1	0.15	0.01
	1000	Int.		+ Mgmt					5	-107.22	224.74	0.86	0.1	0.15	0.01
	1000	Int.			+ (0.10±0.05) PAR		+ (0.09±0.09) SHDI		6	-106.3	225.02	1.14	0.09	0.15	0.01
	1000	Int.		+ Mgmt	+ (0.09±0.05) PAR		+ (0.08±0.09) SHDI		7	-105.28	225.13	1.26	0.08	0.15	0.01
	1000	Int.			+ (0.07±0.06) PAR	+ (0.06±0.07) PSH			6	-106.42	225.26	1.38	0.08	0.15	0.01
	1000	Int.							4	-108.59	225.39	1.51	0.07	0.15	0.00
	1000	Int.				+ (0.11±0.06) PSH	+ (0.11±0.09) SHDI		6	-106.48	225.40	1.52	0.07	0.15	0.00
	1000	Int.		+ Mgmt		+ (0.08±0.06) PSH			6	-106.54	225.50	1.63	0.07	0.15	0.00
	1000	Int.		+ Mgmt	+ (0.08±0.06) PAR	+ (0.03±0.07) PSH			7	-105.63	225.84	1.96	0.06	0.15	0.00

Response	Scale	Model	df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
c) Parasitoid	**100**	**Int. + Mgmt + (0.14±0.06) PAR + Mgmt:PAR**	**7**	**-194.86**	**404.29**	**0**	**0.4**	0.04	0.00
abundance	100	Int. + Mgmt + (0.06±0.03) PAR	6	-196.31	405.05	0.76	0.27	0.04	0.00
	100	Int. + Mgmt + (0.14±0.06) PAR + (0.03±0.04) SHDI + Mgmt:PAR	8	-194.61	405.95	1.66	0.17	0.04	0.00
	100	Int. + Mgmt + (0.15±0.06) PAR + (-0.02±0.03) PSH + Mgmt:PAR	8	-194.69	406.13	1.84	0.16	0.04	0.00
	200	**Int. + Mgmt + (0.11±0.04) PAR + (-0.06±0.03) PSH**	**7**	**-193.54**	**401.65**	**0**	**0.18**	0.00	0.01
	200	Int. + Mgmt + (0.09±0.04) PAR + (0.00±0.06) SHDI + Mgmt:SHDI	8	-192.72	402.18	0.53	0.14	0.00	0.01
	200	Int. + Mgmt + (0.10±0.04) PAR	6	-194.94	402.31	0.66	0.13	0.00	0.01
	200	Int. + Mgmt + (0.11±0.04) PAR + (-0.05±0.03) PSH + (0.05±0.05) SHDI	8	-193	402.74	1.09	0.11	0.00	0.01
	200	Int. + Mgmt + (0.17±0.06) PAR + (-0.06±0.03) PSH + Mgmt:PAR	8	-193.02	402.78	1.13	0.1	0.00	0.01
	200	Int. + Mgmt + (0.11±0.04) PAR + (-0.04±0.03) PSH + (0.01±0.06) SHDI + Mgmt:SHDI	9	-191.94	402.81	1.16	0.1	0.00	0.01
	200	Int. + Mgmt + (0.10±0.04) PAR + (0.05±0.05) SHDI	7	-194.34	403.25	1.6	0.08	0.00	0.00
	200	Int. + Mgmt + (0.15±0.06) PAR + (0.00±0.06) SHDI + Mgmt:PAR + Mgmt:SHDI	9	-192.18	403.30	1.65	0.08	0.00	0.00
	200	Int. + Mgmt + (0.15±0.06) PAR + Mgmt:PAR	7	-194.48	403.53	1.89	0.07	0.00	0.00
	300	**Int. + Mgmt + (0.16±0.04) PAR + (-0.13±0.04) PSH**	**7**	**-190.67**	**395.92**	**0**	**0.71**	0.03	0.18
	300	Int. + Mgmt + (0.15±0.04) PAR + (-0.15±0.06) PSH + Mgmt:PSH	8	-190.5	397.73	1.82	0.29	0.03	0.07
	➡ **400**	**Int. + Mgmt + (0.18±0.05) PAR + (-0.13±0.05) PSH**	**7**	**-190.3**	**395.18**	**0**	**1**	0.03	0.25
	500	**Int. + Mgmt + (0.17±0.05) PAR + (-0.11±0.05) PSH**	**7**	**-191.06**	**396.69**	**0**	**0.54**	0.07	0.12
	500	Int. + Mgmt + (0.17±0.05) PAR + (-0.15±0.07) PSH + Mgmt:PSH	8	-190.8	398.34	1.64	0.24	0.07	0.05
	500	Int. + Mgmt + (0.21±0.08) PAR + (-0.11±0.05) PSH + Mgmt:PAR	8	-190.89	398.51	1.82	0.22	0.07	0.05
	600	**Int. + Mgmt + (0.17±0.05) PAR + (-0.11±0.06) PSH**	**7**	**-192.03**	**398.64**	**0**	**0.71**	0.07	0.04
	600	Int. + Mgmt + (0.21±0.08) PAR + (-0.11±0.06) PSH + Mgmt:PAR	8	-191.85	400.44	1.8	0.29	0.07	0.02
	700	**Int. + Mgmt + (0.19±0.06) PAR + (-0.11±0.06) PSH**	**7**	**-192.66**	**399.88**	**0**	**0.47**	0.09	0.02
	700	Int. + Mgmt + (0.16±0.06) PAR	6	-194.13	400.68	0.8	0.32	0.09	0.02
	700	Int. + Mgmt + (0.24±0.09) PAR + (-0.12±0.06) PSH + Mgmt:PAR	8	-192.4	401.54	1.65	0.21	0.09	0.01
	800	**Int. + Mgmt + (0.20±0.06) PAR + (-0.11±0.07) PSH**	**7**	**-193.18**	**400.94**	**0**	**0.41**	0.32	0.01
	800	Int. + Mgmt + (0.17±0.06) PAR	6	-194.39	401.20	0.27	0.36	0.32	0.01
	800	Int. + Mgmt + (0.28±0.10) PAR + (-0.13±0.07) PSH + Mgmt:PAR	8	-192.71	402.15	1.22	0.23	0.32	0.01
	900	**Int. + Mgmt + (0.22±0.07) PAR + (-0.15±0.09) PSH**	**7**	**-192.94**	**400.46**	**0**	**0.43**	0.14	0.02
	900	Int. + Mgmt + (0.33±0.11) PAR + (-0.17±0.09) PSH + Mgmt:PAR	8	-192.23	401.20	0.73	0.29	0.14	0.01
	900	Int. + Mgmt + (0.17±0.06) PAR	6	-194.44	401.30	0.84	0.28	0.14	0.01
	1000	**Int. + Mgmt + (0.23±0.07) PAR + (-0.16±0.09) PSH**	**7**	**-193.44**	**401.45**	**0**	**0.39**	0.20	0.01
	1000	Int. + Mgmt + (0.36±0.12) PAR + (-0.19±0.1) PSH + Mgmt:PAR	8	-192.54	401.82	0.37	0.32	0.20	0.01
	1000	Int. + Mgmt + (0.17±0.06) PAR	6	-194.82	402.07	0.62	0.29	0.20	0.01

Response	Scale	Model						df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
d) Parasitoid	**100**	**Int. + Mgmt + (0.12±0.04) PAR**			**+ Mgmt:PAR**			**7**	**-143.44**	**301.45**	**0**	**0.72**	0.05	0.00
richness	100	Int. + Mgmt + (0.04±0.02) PAR						6	-145.45	303.32	1.87	0.28	0.05	0.00
	200	**Int. + Mgmt + (0.07±0.03) PAR**						**6**	**-144.14**	**300.70**	**0**	**0.21**	0.00	0.00
	200	Int. + Mgmt + (0.08±0.03) PAR	+ (-0.03±0.03) PSH					7	-143.24	301.04	0.34	0.17	0.00	0.00
	200	Int. + Mgmt + (0.12±0.05) PAR			+ Mgmt:PAR			7	-143.38	301.33	0.63	0.15	0.00	0.00
	200	Int. + Mgmt + (0.07±0.03) PAR		+ (-0.02±0.04) SHDI			+ Mgmt:SHDI	8	-142.36	301.47	0.76	0.14	0.00	0.00
	200	Int. + Mgmt + (0.13±0.05) PAR	+ (-0.04±0.03) PSH		+ Mgmt:PAR			8	-142.42	301.58	0.88	0.13	0.00	0.00
	200	Int. + Mgmt + (0.12±0.05) PAR		+ (-0.02±0.04) SHDI	+ Mgmt:PAR		+ Mgmt:SHDI	9	-141.53	301.98	1.28	0.11	0.00	0.00
	200	Int. + Mgmt + (0.07±0.03) PAR		+ (0.02±0.04) SHDI				7	-143.98	302.54	1.84	0.08	0.00	0.00
	300	**Int. + Mgmt + (0.12±0.03) PAR**	**+ (-0.09±0.03) PSH**					**7**	**-140.34**	**295.26**	**0**	**0.43**	0.02	0.03
	300	Int. + Mgmt + (0.11±0.03) PAR	+ (-0.12±0.05) PSH			+ Mgmt:PSH		8	-140	296.73	1.47	0.21	0.02	0.02
	300	Int. + Mgmt + (0.13±0.04) PAR	+ (-0.10±0.03) PSH	+ (-0.03±0.04) SHDI				8	-140.03	296.80	1.54	0.2	0.02	0.02
	300	Int. + Mgmt + (0.14±0.05) PAR	+ (-0.09±0.03) PSH		+ Mgmt:PAR			8	-140.19	297.12	1.86	0.17	0.02	0.01
➡	**400**	**Int. + Mgmt + (0.14±0.04) PAR**	**+ (-0.11±0.04) PSH**					**7**	**-139**	**292.56**	**0**	**0.51**	0.04	0.13
	400	Int. + Mgmt + (0.15±0.04) PAR	+ (-0.11±0.04) PSH	+ (-0.03±0.03) SHDI				8	-138.52	293.78	1.22	0.28	0.04	0.07
	400	Int. + Mgmt + (0.13±0.04) PAR	+ (-0.13±0.05) PSH			+ Mgmt:PSH		8	-138.77	294.29	1.72	0.21	0.04	0.05
	500	**Int. + Mgmt + (0.13±0.04) PAR**	**+ (-0.10±0.04) PSH**					**7**	**-139.42**	**293.41**	**0**	**0.43**	0.06	0.08
	500	Int. + Mgmt + (0.14±0.04) PAR	+ (-0.10±0.04) PSH	+ (-0.03±0.04) SHDI				8	-139.05	294.84	1.42	0.21	0.06	0.04
	500	Int. + Mgmt + (0.13±0.04) PAR	+ (-0.13±0.05) PSH			+ Mgmt:PSH		8	-139.15	295.03	1.61	0.19	0.06	0.04
	500	Int. + Mgmt + (0.16±0.06) PAR	+ (-0.10±0.04) PSH		+ Mgmt:PAR			8	-139.22	295.17	1.76	0.18	0.06	0.04
	600	**Int. + Mgmt + (0.14±0.04) PAR**	**+ (-0.11±0.04) PSH**					**7**	**-139.63**	**293.82**	**0**	**0.56**	0.10	0.07
	600	Int. + Mgmt + (0.17±0.06) PAR	+ (-0.11±0.04) PSH		+ Mgmt:PAR			8	-139.44	295.62	1.8	0.23	0.10	0.03
	600	Int. + Mgmt + (0.14±0.04) PAR	+ (-0.11±0.04) PSH	+ (-0.02±0.04) SHDI				8	-139.49	295.73	1.9	0.22	0.10	0.03
	700	**Int. + Mgmt + (0.16±0.04) PAR**	**+ (-0.11±0.05) PSH**					**7**	**-139.89**	**294.35**	**0**	**0.55**	0.16	0.05
	700	Int. + Mgmt + (0.20±0.07) PAR	+ (-0.12±0.05) PSH		+ Mgmt:PAR			8	-139.67	296.08	1.72	0.23	0.16	0.02
	700	Int. + Mgmt + (0.16±0.04) PAR	+ (-0.11±0.05) PSH	+ (-0.03±0.05) SHDI				8	-139.73	296.20	1.85	0.22	0.16	0.02
	800	**Int. + Mgmt + (0.17±0.05) PAR**	**+ (-0.12±0.06) PSH**					**7**	**-140.63**	**295.83**	**0**	**0.48**	0.22	0.03
	800	Int. + Mgmt + (0.17±0.05) PAR	+ (-0.12±0.06) PSH	+ (-0.07±0.06) SHDI				8	-140.07	296.88	1.05	0.28	0.22	0.01
	800	Int. + Mgmt + (0.23±0.08) PAR	+ (-0.13±0.06) PSH		+ Mgmt:PAR			8	-140.25	297.24	1.41	0.24	0.22	0.01
	900	**Int. + Mgmt + (0.19±0.05) PAR**	**+ (-0.15±0.07) PSH**					**7**	**-140.27**	**295.11**	**0**	**0.32**	0.16	0.04
	900	Int. + Mgmt + (0.19±0.05) PAR	+ (-0.15±0.07) PSH	+ (-0.09±0.07) SHDI				8	-139.59	295.92	0.81	0.21	0.16	0.02
	900	Int. + Mgmt + (0.27±0.08) PAR	+ (-0.16±0.07) PSH		+ Mgmt:PAR			8	-139.69	296.12	1.01	0.19	0.16	0.02
	900	Int. + Mgmt + (0.19±0.05) PAR	+ (-0.15±0.07) PSH	+ (-0.15±0.09) SHDI			+ Mgmt:SHDI	9	-138.87	296.66	1.55	0.15	0.16	0.02
	900	Int. + Mgmt + (0.26±0.08) PAR	+ (-0.17±0.07) PSH	+ (-0.09±0.07) SHDI	+ Mgmt:PAR			9	-139.02	296.97	1.86	0.13	0.16	0.01
	1000	**Int. + Mgmt + (0.20±0.06) PAR**	**+ (-0.15±0.07) PSH**					**7**	**-140.79**	**296.16**	**0**	**0.3**	0.19	0.02
	1000	Int. + Mgmt + (0.29±0.10) PAR	+ (-0.18±0.07) PSH		+ Mgmt:PAR			8	-140.08	296.90	0.74	0.21	0.19	0.01
	1000	Int. + Mgmt + (0.21±0.06) PAR	+ (-0.17±0.07) PSH	+ (-0.10±0.09) SHDI				8	-140.12	296.98	0.83	0.2	0.19	0.01
	1000	Int. + Mgmt + (0.30±0.09) PAR	+ (-0.19±0.08) PSH	+ (-0.11±0.09) SHDI	+ Mgmt:PAR			9	-139.3	297.52	1.36	0.15	0.19	0.01
	1000	Int. + Mgmt + (0.21±0.06) PAR	+ (-0.17±0.07) PSH	+ (-0.18±0.11) SHDI			+ Mgmt:SHDI	9	-139.36	297.65	1.5	0.14	0.19	0.01

Response	Scale	Model									df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
e) Predatory wasp abundance	**100**	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.05±0.03) PAR**	**+ (0.13±0.04) PSH**	**+ (0.08±0.04) SHDI**		**+ Mgmt:PSH**		**13**	**-155.27**	**338.46**	**0**	**0.35**	0.00	0.03
	100	Int.	+ Crop	+ Mgmt		+ (0.15±0.04) PSH	+ (0.07±0.04) SHDI		+ Mgmt:PSH		12	-157.02	339.67	1.21	0.19	0.00	0.02
	100	Int.	+ Crop	+ Mgmt	+ (0.04±0.03) PAR	+ (0.13±0.04) PSH			+ Mgmt:PSH		12	-157.21	340.05	1.59	0.16	0.00	0.01
	100	Int.	+ Crop	+ Mgmt	+ (0.09±0.06) PAR	+ (0.12±0.04) PSH	+ (0.08±0.04) SHDI	+ Mgmt:PAR	+ Mgmt:PSH		14	-154.98	340.19	1.73	0.15	0.00	0.01
	100	Int.	+ Crop	+ Mgmt		+ (0.14±0.04) PSH			+ Mgmt:PSH		11	-158.42	340.22	1.76	0.15	0.00	0.01
	200	**Int.**			**+ (0.10±0.03) PAR**						**5**	**-166.28**	**342.85**	**0**	**0.16**	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.17±0.06) PAR	+ (0.11±0.05) PSH		+ Mgmt:PAR	+ Mgmt:PSH		13	-157.58	343.07	0.22	0.15	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.19±0.06) PAR			+ Mgmt:PAR			11	-159.89	343.16	0.31	0.14	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.09±0.03) PAR	+ (0.13±0.05) PSH			+ Mgmt:PSH		12	-158.87	343.38	0.52	0.12	0.00	0.00
	200	Int.		+ Mgmt	+ (0.18±0.06) PAR			+ Mgmt:PAR			7	-164.47	343.51	0.65	0.12	0.00	0.00
	200	Int.	+ Crop		+ (0.09±0.03) PAR						9	-162.37	343.67	0.82	0.11	0.00	0.00
	200	Int.			+ (0.09±0.04) PAR	+ (0.03±0.03) PSH					6	-165.94	344.30	1.45	0.08	0.00	0.00
	200	Int.		+ Mgmt	+ (0.09±0.04) PAR						6	-166.11	344.64	1.78	0.07	0.00	0.00
	200	Int.		+ Mgmt	+ (0.08±0.03) PAR	+ (0.11±0.05) PSH			+ Mgmt:PSH		8	-164.03	344.80	1.95	0.06	0.00	0.00
	300	**Int.**			**+ (0.11±0.04) PAR**						**5**	**-166.09**	**342.49**	**0**	**0.28**	0.00	0.00
	300	Int.			+ (0.13±0.04) PAR		+ (-0.05±0.04) SHDI				6	-165.37	343.17	0.68	0.2	0.00	0.00
	300	Int.	+ Crop		+ (0.11±0.04) PAR						9	-162.44	343.80	1.31	0.15	0.00	0.00
	300	Int.			+ (0.10±0.04) PAR	+ (0.03±0.04) PSH					6	-165.76	343.94	1.45	0.14	0.00	0.00
	300	Int.		+ Mgmt	+ (0.19±0.06) PAR			+ Mgmt:PAR			7	-164.83	344.22	1.74	0.12	0.00	0.00
	300	Int.		+ Mgmt	+ (0.11±0.04) PAR						6	-165.95	344.32	1.83	0.11	0.00	0.00
	400	**Int.**			**+ (0.13±0.05) PAR**						**5**	**-166.18**	**342.66**	**0**	**0.19**	0.00	0.00
	400	Int.			+ (0.15±0.05) PAR		+ (-0.06±0.04) SHDI				6	-165.12	342.67	0.01	0.19	0.00	0.00
	400	Int.			+ (0.12±0.05) PAR	+ (0.06±0.04) PSH					6	-165.4	343.22	0.57	0.14	0.00	0.00
	400	Int.			+ (0.13±0.05) PAR	+ (0.05±0.04) PSH	+ (-0.06±0.04) SHDI				7	-164.37	343.32	0.66	0.14	0.00	0.00
	400	Int.	+ Crop		+ (0.13±0.04) PAR						9	-162.56	344.05	1.4	0.1	0.00	0.00
	400	Int.		+ Mgmt	+ (0.14±0.05) PAR		+ (-0.06±0.04) SHDI				7	-164.88	344.34	1.68	0.08	0.00	0.00
	400	Int.		+ Mgmt	+ (0.12±0.05) PAR						6	-165.96	344.34	1.68	0.08	0.00	0.00
	400	Int.	+ Crop		+ (0.11±0.05) PAR	+ (0.05±0.04) PSH					10	-161.72	344.59	1.93	0.07	0.00	0.00
	500	**Int.**			**+ (0.15±0.05) PAR**		**+ (-0.07±0.05) SHDI**				**6**	**-165.19**	**342.80**	**0**	**0.21**	0.01	0.00
	500	Int.			+ (0.13±0.05) PAR						5	-166.28	342.86	0.05	0.21	0.01	0.00
	500	Int.			+ (0.14±0.05) PAR	+ (0.06±0.04) PSH	+ (-0.07±0.04) SHDI				7	-164.42	343.41	0.61	0.16	0.01	0.00
	500	Int.			+ (0.12±0.05) PAR	+ (0.05±0.05) PSH					6	-165.65	343.73	0.93	0.13	0.01	0.00
	500	Int.		+ Mgmt	+ (0.14±0.05) PAR		+ (-0.07±0.05) SHDI				7	-164.75	344.08	1.27	0.11	0.01	0.00
	500	Int.		+ Mgmt	+ (0.13±0.05) PAR						6	-166	344.43	1.63	0.09	0.01	0.00
	500	Int.		+ Mgmt	+ (0.16±0.05) PAR		+ (-0.02±0.06) SHDI			+ Mgmt:SHDI	8	-164.03	344.79	1.99	0.08	0.01	0.00
	600	**Int.**			**+ (0.14±0.05) PAR**						**5**	**-166.21**	**342.72**	**0**	**0.17**	0.01	0.00
	600	Int.			+ (0.15±0.05) PAR		+ (-0.07±0.05) SHDI				6	-165.17	342.77	0.05	0.16	0.01	0.00
	600	Int.		+ Mgmt	+ (0.16±0.05) PAR		+ (-0.02±0.06) SHDI			+ Mgmt:SHDI	8	-163.18	343.09	0.38	0.14	0.01	0.00
	600	Int.		+ Mgmt	+ (0.14±0.05) PAR		+ (-0.08±0.05) SHDI				7	-164.44	343.45	0.73	0.12	0.01	0.00
	600	Int.			+ (0.14±0.05) PAR	+ (0.06±0.05) PSH	+ (-0.08±0.05) SHDI				7	-164.51	343.59	0.88	0.11	0.01	0.00
	600	Int.			+ (0.13±0.05) PAR	+ (0.04±0.05) PSH					6	-165.83	344.09	1.38	0.08	0.01	0.00
	600	Int.		+ Mgmt	+ (0.14±0.05) PAR						6	-165.84	344.10	1.38	0.08	0.01	0.00
	600	Int.		+ Mgmt	+ (0.15±0.05) PAR	+ (0.05±0.05) PSH	+ (-0.02±0.06) SHDI			+ Mgmt:SHDI	9	-162.67	344.27	1.55	0.08	0.01	0.00
	600	Int.		+ Mgmt	+ (0.21±0.07) PAR		+ (-0.01±0.06) SHDI	+ Mgmt:PAR		+ Mgmt:SHDI	9	-162.76	344.44	1.73	0.07	0.01	0.00

700	**Int.**		**+ (0.16±0.05) PAR**					**5**	**-165.62**	**341.55**	**0**	**0.19**	0.01	0.01
700	Int.		+ (0.16±0.05) PAR		+ (-0.08±0.06) SHDI			6	-164.61	341.64	0.09	0.18	0.01	0.01
700	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.02±0.07) SHDI		+ Mgmt:SHDI	8	-162.55	341.84	0.29	0.16	0.01	0.01
700	Int.	+ Mgmt	+ (0.16±0.05) PAR		+ (-0.10±0.06) SHDI			7	-163.85	342.27	0.72	0.13	0.01	0.00
700	Int.	+ Mgmt	+ (0.16±0.05) PAR					6	-165.23	342.89	1.34	0.1	0.01	0.00
700	Int.	+ Mgmt	+ (0.22±0.07) PAR		+ (-0.02±0.07) SHDI	+ Mgmt:PAR	+ Mgmt:SHDI	9	-162.15	343.23	1.68	0.08	0.01	0.00
700	Int.		+ (0.15±0.05) PAR	+ (0.04±0.06) PSH	+ (-0.09±0.06) SHDI			7	-164.38	343.33	1.78	0.08	0.01	0.00
700	Int.		+ (0.16±0.05) PAR	+ (0.02±0.06) PSH				6	-165.53	343.49	1.94	0.07	0.01	0.00
800	**Int.**		**+ (0.18±0.05) PAR**		**+ (-0.14±0.07) SHDI**			**6**	**-163.55**	**339.52**	**0**	**0.27**	0.77	0.02
800	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.16±0.07) SHDI			7	-162.67	339.90	0.38	0.23	0.77	0.01
800	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.09±0.09) SHDI		+ Mgmt:SHDI	8	-161.89	340.53	1	0.17	0.77	0.01
800	Int.		+ (0.18±0.05) PAR					5	-165.48	341.25	1.73	0.12	0.77	0.01
800	Int.		+ (0.16±0.06) PAR	+ (0.04±0.06) PSH	+ (-0.14±0.07) SHDI			7	-163.38	341.33	1.8	0.11	0.77	0.01
800	Int.	+ Mgmt	+ (0.22±0.08) PAR		+ (-0.15±0.07) SHDI	+ Mgmt:PAR		8	-162.33	341.41	1.88	0.11	0.77	0.01
➡ **900**	**Int.**		**+ (0.18±0.05) PAR**		**+ (-0.23±0.08) SHDI**			**6**	**-161.51**	**335.45**	**0**	**0.32**	0.02	0.14
900	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.25±0.08) SHDI			7	-160.61	335.79	0.34	0.27	0.02	0.11
900	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.18±0.10) SHDI		+ Mgmt:SHDI	8	-160.1	336.94	1.5	0.15	0.02	0.06
900	Int.	+ Mgmt	+ (0.23±0.08) PAR		+ (-0.24±0.08) SHDI	+ Mgmt:PAR		8	-160.21	337.16	1.71	0.13	0.02	0.06
900	Int.		+ (0.17±0.06) PAR	+ (0.04±0.07) PSH	+ (-0.23±0.08) SHDI			7	-161.32	337.22	1.77	0.13	0.02	0.06
1000	**Int.**		**+ (0.18±0.06) PAR**		**+ (-0.29±0.10) SHDI**			**6**	**-161.89**	**336.20**	**0**	**0.32**	0.17	0.09
1000	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.30±0.10) SHDI			7	-160.96	336.50	0.3	0.27	0.17	0.08
1000	Int.	+ Mgmt	+ (0.17±0.05) PAR		+ (-0.23±0.12) SHDI		+ Mgmt:SHDI	8	-160.42	337.57	1.37	0.16	0.17	0.05
1000	Int.	+ Mgmt	+ (0.23±0.09) PAR		+ (-0.31±0.10) SHDI	+ Mgmt:PAR		8	-160.62	337.98	1.78	0.13	0.17	0.04
1000	Int.		+ (0.17±0.06) PAR	+ (0.03±0.08) PSH	+ (-0.29±0.10) SHDI			7	-161.79	338.15	1.95	0.12	0.17	0.04

Response	Scale	Model								df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
f) Predatory	**100**	**Int.**		**+ Mgmt**		**+ (0.11±0.03) PSH**			**+ Mgmt:PSH**	**7**	**-129.88**	**274.33**	**0**	**0.36**	0.01	0.04
wasp richness	100	Int.	+ Crop	+ Mgmt		+ (0.13±0.03) PSH			+ Mgmt:PSH	11	-125.93	275.24	0.91	0.23	0.01	0.02
	100	Int.		+ Mgmt	+ (0.02±0.02) PAR	+ (0.10±0.03) PSH			+ Mgmt:PSH	8	-129.26	275.27	0.94	0.23	0.01	0.02
	100	Int.	+ Crop	+ Mgmt	+ (0.03±0.02) PAR	+ (0.12±0.03) PSH			+ Mgmt:PSH	12	-125.03	275.68	1.35	0.18	0.01	0.02
	200	**Int.**		**+ Mgmt**	**+ (0.06±0.03) PAR**	**+ (0.12±0.04) PSH**			**+ Mgmt:PSH**	**8**	**-130.01**	**276.75**	**0**	**0.24**	0.00	0.01
	200	Int.	+ Crop	+ Mgmt	+ (0.07±0.03) PAR	+ (0.14±0.04) PSH			+ Mgmt:PSH	12	-125.67	276.97	0.22	0.22	0.00	0.01
	200	Int.		+ Mgmt	+ (0.06±0.03) PAR	+ (0.12±0.04) PSH	+ (-0.04±0.04) SHDI		+ Mgmt:PSH	9	-129.46	277.85	1.1	0.14	0.00	0.01
	200	Int.		+ Mgmt	+ (0.09±0.05) PAR	+ (0.11±0.04) PSH		+ Mgmt:PAR	+ Mgmt:PSH	9	-129.74	278.41	1.66	0.11	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.11±0.05) PAR	+ (0.13±0.04) PSH		+ Mgmt:PAR	+ Mgmt:PSH	13	-125.25	278.42	1.67	0.1	0.00	0.00
	200	Int.			+ (0.08±0.03) PAR					5	-134.08	278.46	1.71	0.1	0.00	0.00
	200	Int.	+ Crop	+ Mgmt	+ (0.07±0.03) PAR	+ (0.14±0.04) PSH	+ (-0.03±0.04) SHDI		+ Mgmt:PSH	13	-125.36	278.63	1.88	0.09	0.00	0.00
	300	**Int.**			**+ (0.11±0.03) PAR**		**+ (-0.05±0.04) SHDI**			**6**	**-132.54**	**277.51**	**0**	**0.22**	0.00	0.01
	300	Int.			+ (0.09±0.03) PAR					5	-133.62	277.54	0.03	0.22	0.00	0.01
	300	Int.			+ (0.08±0.03) PAR	+ (0.04±0.03) PSH				6	-132.89	278.20	0.68	0.16	0.00	0.01
	300	Int.			+ (0.09±0.03) PAR	+ (0.03±0.03) PSH	+ (-0.05±0.04) SHDI			7	-132.03	278.63	1.11	0.13	0.00	0.00
	300	Int.		+ Mgmt	+ (0.09±0.03) PAR					6	-133.37	279.16	1.65	0.1	0.00	0.00
	300	Int.		+ Mgmt	+ (0.10±0.03) PAR		+ (-0.05±0.04) SHDI			7	-132.35	279.27	1.75	0.09	0.00	0.00
	300	Int.		+ Mgmt	+ (0.15±0.05) PAR			+ Mgmt:PAR		7	-132.39	279.36	1.85	0.09	0.00	0.00
	400	**Int.**			**+ (0.10±0.04) PAR**	**+ (0.06±0.03) PSH**	**+ (-0.05±0.03) SHDI**			**7**	**-131.32**	**277.21**	**0**	**0.23**	0.00	0.01
	400	Int.			+ (0.09±0.04) PAR	+ (0.06±0.03) PSH				6	-132.39	277.21	0	0.23	0.00	0.01
	400	Int.			+ (0.12±0.04) PAR		+ (-0.05±0.03) SHDI			6	-132.92	278.26	1.05	0.13	0.00	0.01
	400	Int.			+ (0.10±0.04) PAR					5	-134.02	278.35	1.14	0.13	0.00	0.00
	400	Int.		+ Mgmt	+ (0.15±0.06) PAR	+ (0.07±0.04) PSH		+ Mgmt:PAR		8	-131.01	278.75	1.54	0.1	0.00	0.00
	400	Int.		+ Mgmt	+ (0.10±0.04) PAR	+ (0.06±0.03) PSH	+ (-0.05±0.03) SHDI			8	-131.13	279.00	1.79	0.09	0.00	0.00
	400	Int.		+ Mgmt	+ (0.08±0.04) PAR	+ (0.06±0.04) PSH				7	-132.22	279.01	1.8	0.09	0.00	0.00
	500	**Int.**			**+ (0.10±0.04) PAR**	**+ (0.07±0.04) PSH**	**+ (-0.06±0.04) SHDI**			**7**	**-131.48**	**277.53**	**0**	**0.3**	0.01	0.01
	500	Int.			+ (0.09±0.04) PAR	+ (0.06±0.04) PSH				6	-132.71	277.84	0.31	0.25	0.01	0.01
	500	Int.			+ (0.11±0.04) PAR					5	-134.22	278.75	1.21	0.16	0.01	0.00
	500	Int.			+ (0.12±0.04) PAR		+ (-0.05±0.04) SHDI			6	-133.23	278.88	1.35	0.15	0.01	0.00
	500	Int.		+ Mgmt	+ (0.10±0.04) PAR	+ (0.06±0.04) PSH	+ (-0.06±0.04) SHDI			8	-131.18	279.10	1.56	0.14	0.01	0.00
	600	**Int.**			**+ (0.10±0.04) PAR**	**+ (0.07±0.04) PSH**	**+ (-0.07±0.04) SHDI**			**7**	**-131.74**	**278.04**	**0**	**0.22**	0.01	0.01
	600	Int.			+ (0.10±0.04) PAR	+ (0.06±0.04) PSH				6	-133.1	278.62	0.57	0.17	0.01	0.00
	600	Int.			+ (0.11±0.04) PAR					5	-134.25	278.81	0.77	0.15	0.01	0.00
	600	Int.			+ (0.11±0.04) PAR		+ (-0.05±0.04) SHDI			6	-133.38	279.18	1.13	0.13	0.01	0.00
	600	Int.		+ Mgmt	+ (0.10±0.04) PAR	+ (0.06±0.04) PSH	+ (-0.07±0.04) SHDI			8	-131.26	279.27	1.22	0.12	0.01	0.00
	600	Int.		+ Mgmt	+ (0.11±0.04) PAR		+ (-0.07±0.04) SHDI			7	-132.42	279.41	1.36	0.11	0.01	0.00
	600	Int.		+ Mgmt	+ (0.10±0.04) PAR					6	-133.7	279.83	1.79	0.09	0.01	0.00
	700	**Int.**			**+ (0.12±0.04) PAR**					**5**	**-133.92**	**278.13**	**0**	**0.16**	0.02	0.01
	700	Int.			+ (0.12±0.04) PAR		+ (-0.06±0.05) SHDI			6	-133.02	278.48	0.34	0.14	0.02	0.00
	700	Int.			+ (0.11±0.04) PAR	+ (0.07±0.05) PSH	+ (-0.07±0.05) SHDI			7	-132.01	278.59	0.46	0.13	0.02	0.00
	700	Int.		+ Mgmt	+ (0.12±0.04) PAR		+ (-0.08±0.05) SHDI			7	-132.02	278.61	0.47	0.13	0.02	0.00
	700	Int.			+ (0.11±0.04) PAR	+ (0.05±0.05) PSH				6	-133.24	278.91	0.77	0.11	0.02	0.00
	700	Int.		+ Mgmt	+ (0.12±0.04) PAR					6	-133.33	279.09	0.96	0.1	0.02	0.00
	700	Int.		+ Mgmt	+ (0.10±0.04) PAR	+ (0.05±0.05) PSH	+ (-0.08±0.05) SHDI			8	-131.43	279.61	1.47	0.08	0.02	0.00
	700	Int.		+ Mgmt	+ (0.17±0.06) PAR		+ (-0.07±0.05) SHDI	+ Mgmt:PAR		8	-131.5	279.74	1.6	0.07	0.02	0.00
	700	Int.		+ Mgmt	+ (0.18±0.06) PAR			+ Mgmt:PAR		7	-132.61	279.80	1.66	0.07	0.02	0.00

	800	**Int.**	**+ Mgmt**	**+ (0.12±0.04) PAR**		**+ (-0.13±0.06) SHDI**		**7**	**-131.02**	**276.61**	**0**	**0.24**	0.47	0.01
	800	Int.		+ (0.13±0.04) PAR		+ (-0.11±0.06) SHDI		6	-132.16	276.75	0.14	0.22	0.47	0.01
	800	Int.		+ (0.11±0.05) PAR	+ (0.06±0.05) PSH	+ (-0.12±0.06) SHDI		7	-131.35	277.27	0.66	0.17	0.47	0.01
	800	Int.	+ Mgmt	+ (0.18±0.07) PAR		+ (-0.12±0.06) SHDI	+ Mgmt:PAR	8	-130.45	277.63	1.03	0.14	0.47	0.01
	800	Int.		+ (0.13±0.05) PAR				5	-133.86	278.02	1.42	0.12	0.47	0.01
	800	Int.	+ Mgmt	+ (0.11±0.05) PAR	+ (0.04±0.05) PSH	+ (-0.13±0.06) SHDI		8	-130.69	278.12	1.51	0.11	0.47	0.01
➡	**900**	**Int.**	**+ Mgmt**	**+ (0.12±0.04) PAR**		**+ (-0.21±0.07) SHDI**		**7**	**-129.13**	**272.84**	**0**	**0.27**	0.02	0.08
	900	Int.		+ (0.13±0.04) PAR		+ (-0.19±0.07) SHDI		6	-130.28	272.99	0.15	0.25	0.02	0.07
	900	Int.		+ (0.11±0.05) PAR	+ (0.07±0.06) PSH	+ (-0.19±0.07) SHDI		7	-129.47	273.52	0.68	0.19	0.02	0.06
	900	Int.	+ Mgmt	+ (0.19±0.07) PAR		+ (-0.20±0.07) SHDI	+ Mgmt:PAR	8	-128.51	273.77	0.93	0.17	0.02	0.05
	900	Int.	+ Mgmt	+ (0.11±0.05) PAR	+ (0.05±0.06) PSH	+ (-0.20±0.07) SHDI		8	-128.87	274.48	1.64	0.12	0.02	0.03
	1000	**Int.**	**+ Mgmt**	**+ (0.12±0.05) PAR**		**+ (-0.27±0.08) SHDI**		**7**	**-128.86**	**272.28**	**0**	**0.3**	0.45	0.10
	1000	Int.		+ (0.13±0.05) PAR		+ (-0.26±0.08) SHDI		6	-130.09	272.60	0.32	0.25	0.45	0.09
	1000	Int.	+ Mgmt	+ (0.18±0.08) PAR		+ (-0.27±0.08) SHDI	+ Mgmt:PAR	8	-128.31	273.35	1.07	0.17	0.45	0.06
	1000	Int.		+ (0.10±0.05) PAR	+ (0.07±0.06) PSH	+ (-0.25±0.08) SHDI		7	-129.47	273.51	1.23	0.16	0.45	0.06
	1000	Int.	+ Mgmt	+ (0.11±0.05) PAR	+ (0.04±0.07) PSH	+ (-0.26±0.08) SHDI		8	-128.71	274.15	1.87	0.12	0.45	0.04

Response	Scale	Model							df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
g) Carabid abundance	**100**	**Int.**	**+ Crop**						**8**	**-68.65**	**156.30**	**0**	**0.47**	0.02	0.01
	100	Int.	+ Crop			+ (0.12±0.08) PSH			9	-67.61	157.06	0.76	0.32	0.02	0.01
	100	Int.	+ Crop				+ (-0.15±0.13) SHDI		9	-68.03	157.89	1.59	0.21	0.02	0.00
	200	**Int.**	**+ Crop**			**+ (0.18±0.09) PSH**			**9**	**-66.96**	**155.75**	**0**	**0.57**	0.00	0.01
	200	Int.	+ Crop						8	-68.65	156.30	0.55	0.43	0.00	0.01
	300	**Int.**	**+ Crop**			**+ (0.26±0.11) PSH**			**9**	**-66.31**	**154.45**	**0**	**0.53**	0.01	0.03
	300	Int.	+ Crop			+ (0.25±0.11) PSH	+ (-0.17±0.13) SHDI		10	-65.56	155.90	1.45	0.26	0.01	0.01
	300	Int.	+ Crop						8	-68.65	156.30	1.85	0.21	0.01	0.01
➡	**400**	**Int.**	**+ Crop**			**+ (0.36±0.11) PSH**	**+ (-0.23±0.11) SHDI**		**10**	**-63.13**	**151.05**	**0**	**0.59**	0.01	0.14
	400	Int.	+ Crop			+ (0.35±0.12) PSH			9	-64.98	151.79	0.74	0.41	0.01	0.10
	500	**Int.**	**+ Crop**			**+ (0.37±0.12) PSH**	**+ (-0.23±0.12) SHDI**		**10**	**-64.13**	**153.05**	**0**	**0.52**	0.03	0.05
	500	Int.	+ Crop			+ (0.34±0.13) PSH			9	-65.71	153.24	0.19	0.48	0.03	0.05
	600	**Int.**	**+ Crop**			**+ (0.41±0.13) PSH**	**+ (-0.27±0.13) SHDI**		**10**	**-64.15**	**153.08**	**0**	**0.61**	0.03	0.05
	600	Int.	+ Crop			+ (0.34±0.14) PSH			9	-66.06	153.95	0.87	0.39	0.03	0.03
	700	**Int.**	**+ Crop**			**+ (0.43±0.14) PSH**	**+ (-0.32±0.15) SHDI**		**10**	**-64.03**	**152.84**	**0**	**0.65**	0.07	0.06
	700	Int.	+ Crop			+ (0.37±0.15) PSH			9	-66.12	154.07	1.23	0.35	0.07	0.03
	800	**Int.**	**+ Crop**			**+ (0.42±0.16) PSH**	**+ (-0.36±0.19) SHDI**		**10**	**-64.65**	**154.08**	**0**	**0.54**	0.44	0.03
	800	Int.	+ Crop			+ (0.38±0.16) PSH			9	-66.28	154.38	0.3	0.46	0.44	0.03
	900	**Int.**	**+ Crop**			**+ (0.48±0.18) PSH**	**+ (-0.45±0.23) SHDI**		**10**	**-64.5**	**153.78**	**0**	**0.58**	0.09	0.04
	900	Int.	+ Crop			+ (0.44±0.19) PSH			9	-66.28	154.40	0.62	0.42	0.09	0.03
	1000	**Int.**	**+ Crop**			**+ (0.54±0.19) PSH**	**+ (-0.49±0.26) SHDI**		**10**	**-64.03**	**152.83**	**0**	**0.21**	0.29	0.06
	1000	Int.	+ Crop		+ (-0.38±0.21) PAR	+ (0.69±0.21) PSH			10	-64.12	153.03	0.19	0.19	0.29	0.05
	1000	Int.	+ Crop			+ (0.53±0.20) PSH			9	-65.71	153.25	0.42	0.17	0.29	0.05
	1000	Int.	+ Crop	+ Mgmt	+ (-0.53±0.20) PAR	+ (1.18±0.28) PSH		+ Mgmt:PSH	12	-61.31	153.72	0.88	0.13	0.29	0.04
	1000	Int.	+ Crop		+ (-0.30±0.20) PAR	+ (0.66±0.20) PSH	+ (-0.40±0.25) SHDI		11	-62.97	153.80	0.97	0.13	0.29	0.04
	1000	Int.	+ Crop	+ Mgmt	+ (-0.43±0.21) PAR	+ (0.78±0.22) PSH			11	-63.33	154.53	1.69	0.09	0.29	0.02
	1000	Int.	+ Crop	+ Mgmt	+ (-0.46±0.20) PAR	+ (1.13±0.27) PSH	+ (-0.37±0.24) SHDI	+ Mgmt:PSH	13	-60.17	154.81	1.97	0.08	0.29	0.02

Response	Scale	Model	df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
h) Carabid richness	**100**	**Int. + Crop + (0.1±0.05) PSH**	**9**	**-40.61**	**103.05**	**0**	**0.61**	0.06	0.05
	100	Int. + Crop	8	-42.48	103.97	0.91	0.39	0.06	0.03
	200	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.6**	0.00	0.03
	200	Int. + Crop + (0.09±0.06) PSH	9	-41.46	104.74	0.78	0.4	0.00	0.02
	300	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.46**	0.01	0.03
	300	Int. + Crop + (-0.13±0.09) SHDI	9	-41.48	104.79	0.83	0.3	0.01	0.02
	300	Int. + Crop + (0.10±0.07) PSH	9	-41.69	105.22	1.25	0.24	0.01	0.02
	➡ **400**	**Int. + Crop + (0.15±0.07) PSH + (-0.16±0.08) SHDI**	**10**	**-39.11**	**103.01**	**0**	**0.34**	0.01	0.05
	400	Int. + Crop + (-0.16±0.08) SHDI	9	-40.88	103.60	0.59	0.25	0.01	0.04
	400	Int. + Crop	8	-42.48	103.97	0.96	0.21	0.01	0.03
	400	Int. + Crop + (0.14±0.08) PSH	9	-41.1	104.03	1.03	0.2	0.01	0.03
	500	**Int. + Crop + (0.15±0.08) PSH + (-0.16±0.08) SHDI**	**10**	**-39.58**	**103.94**	**0**	**0.28**	0.07	0.03
	500	Int. + Crop	8	-42.48	103.97	0.03	0.28	0.07	0.03
	500	Int. + Crop + (-0.15±0.09) SHDI	9	-41.21	104.24	0.3	0.24	0.07	0.03
	500	Int. + Crop + (0.13±0.09) PSH	9	-41.4	104.62	0.68	0.2	0.07	0.02
	600	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.32**	0.08	0.03
	600	Int. + Crop + (0.17±0.09) PSH + (-0.18±0.09) SHDI	10	-39.8	104.39	0.43	0.26	0.08	0.03
	600	Int. + Crop + (-0.14±0.10) SHDI	9	-41.43	104.69	0.72	0.23	0.08	0.02
	600	Int. + Crop + (0.13±0.09) PSH	9	-41.61	105.06	1.09	0.19	0.08	0.02
	700	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.32**	0.09	0.03
	700	Int. + Crop + (-0.17±0.11) SHDI	9	-41.29	104.41	0.44	0.25	0.09	0.03
	700	Int. + Crop + (0.17±0.10) PSH + (-0.2±0.10) SHDI	10	-39.82	104.42	0.46	0.25	0.09	0.03
	700	Int. + Crop + (0.13±0.10) PSH	9	-41.66	105.15	1.19	0.18	0.09	0.02
	800	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.34**	0.34	0.03
	800	Int. + Crop + (-0.21±0.13) SHDI	9	-41.37	104.57	0.6	0.25	0.34	0.02
	800	Int. + Crop + (0.17±0.10) PSH + (-0.23±0.13) SHDI	10	-40.06	104.90	0.94	0.21	0.34	0.02
	800	Int. + Crop + (0.15±0.11) PSH	9	-41.62	105.07	1.11	0.2	0.34	0.02
	900	**Int. + Crop**	**8**	**-42.48**	**103.97**	**0**	**0.31**	0.15	0.03
	900	Int. + Crop + (-0.28±0.16) SHDI	9	-41.14	104.11	0.15	0.29	0.15	0.03
	900	Int. + Crop + (0.19±0.12) PSH + (-0.30±0.15) SHDI	10	-39.91	104.59	0.63	0.23	0.15	0.02
	900	Int. + Crop + (0.17±0.13) PSH	9	-41.64	105.10	1.14	0.18	0.15	0.02
	1000	**Int. + Crop + (-0.33±0.19) SHDI**	**9**	**-41.01**	**103.85**	**0**	**0.3**	0.19	0.03
	1000	Int. + Crop	8	-42.48	103.97	0.12	0.29	0.19	0.03
	1000	Int. + Crop + (0.20±0.13) PSH + (-0.33±0.17) SHDI	10	-39.87	104.52	0.67	0.22	0.19	0.02
	1000	Int. + Crop + (0.20±0.14) PSH	9	-41.48	104.79	0.94	0.19	0.19	0.02

Response	Scale	Model								df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
i) Staphylinid abundance	**100**	**Int.**								**4**	**-70.09**	**148.96**	**0**	**0.39**	0.01	0.00
	100	Int.	+ Crop							8	-65.4	149.81	0.85	0.25	0.01	0.00
	100	Int.	+ Crop			+ (0.14±0.09) PSH				9	-64.2	150.23	1.27	0.2	0.01	0.00
	100	Int.		+ Mgmt						5	-69.77	150.72	1.77	0.16	0.01	0.00
	200	**Int.**								**4**	**-70.09**	**148.96**	**0**	**0.31**	0.00	0.00
	200	Int.	+ Crop							8	-65.4	149.81	0.85	0.2	0.00	0.00
	200	Int.		+ Mgmt						5	-69.77	150.72	1.77	0.13	0.00	0.00
	200	Int.			+ (0.09±0.13) PAR					5	-69.83	150.83	1.88	0.12	0.00	0.00
	200	Int.	+ Crop		+ (0.17±0.12) PAR					9	-64.51	150.85	1.9	0.12	0.00	0.00
	200	Int.				+ (0.08±0.11) PSH				5	-69.85	150.87	1.91	0.12	0.00	0.00
	300	**Int.**	**+ Crop**		**+ (0.29±0.13) PAR**		**+ (-0.29±0.13) SHDI**			**10**	**-62**	**148.78**	**0**	**0.12**	0.00	0.00
	300	Int.								4	-70.09	148.96	0.17	0.11	0.00	0.00
	300	Int.	+ Crop	+ Mgmt	+ (0.32±0.12) PAR		+ (-0.32±0.13) SHDI			11	-60.55	148.97	0.19	0.11	0.00	0.00
	300	Int.					+ (-0.24±0.16) SHDI			5	-69.1	149.39	0.61	0.09	0.00	0.00
	300	Int.	+ Crop	+ Mgmt	+ (0.51±0.17) PAR		+ (-0.28±0.12) SHDI	+ Mgmt:PAR		12	-59.19	149.48	0.69	0.09	0.00	0.00
	300	Int.	+ Crop							8	-65.4	149.81	1.03	0.07	0.00	0.00
	300	Int.	+ Crop		+ (0.25±0.14) PAR					9	-64.05	149.93	1.15	0.07	0.00	0.00
	300	Int.	+ Crop				+ (-0.25±0.15) SHDI			9	-64.13	150.08	1.3	0.06	0.00	0.00
	300	Int.			+ (0.15±0.15) PAR					5	-69.6	150.37	1.59	0.06	0.00	0.00
	300	Int.			+ (0.17±0.14) PAR		+ (-0.26±0.16) SHDI			6	-68.37	150.43	1.65	0.05	0.00	0.00
	300	Int.	+ Crop	+ Mgmt	+ (0.53±0.19) PAR			+ Mgmt:PAR		11	-61.33	150.53	1.75	0.05	0.00	0.00
	300	Int.		+ Mgmt			+ (-0.28±0.16) SHDI			6	-68.47	150.63	1.85	0.05	0.00	0.00
	300	Int.		+ Mgmt						5	-69.77	150.72	1.94	0.05	0.00	0.00
	➡ **400**	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.46±0.13) PAR**		**+ (-0.28±0.12) SHDI**		**+ Mgmt:SHDI**	**12**	**-55.62**	**142.33**	**0**	**0.41**	0.01	0.09
	400	Int.	+ Crop		+ (0.37±0.13) PAR		+ (-0.41±0.11) SHDI			10	-58.89	142.56	0.24	0.36	0.01	0.08
	400	Int.	+ Crop	+ Mgmt	+ (0.39±0.13) PAR		+ (-0.41±0.11) SHDI			11	-57.81	143.49	1.16	0.23	0.01	0.05
	500	**Int.**	**+ Crop**		**+ (0.35±0.14) PAR**		**+ (-0.44±0.12) SHDI**			**10**	**-58.94**	**142.66**	**0**	**0.71**	0.03	0.07
	500	Int.					+ (-0.42±0.15) SHDI			5	-66.62	144.42	1.76	0.29	0.03	0.03
	600	**Int.**	**+ Crop**		**+ (0.31±0.14) PAR**		**+ (-0.46±0.13) SHDI**			**10**	**-59.55**	**143.87**	**0**	**0.36**	0.03	0.04
	600	Int.					+ (-0.45±0.16) SHDI			5	-66.72	144.61	0.74	0.25	0.03	0.03
	600	Int.	+ Crop				+ (-0.44±0.15) SHDI			9	-61.54	144.92	1.04	0.22	0.03	0.02
	600	Int.			+ (0.20±0.15) PAR		+ (-0.45±0.16) SHDI			6	-65.88	145.44	1.57	0.17	0.03	0.02
	700	**Int.**					**+ (-0.53±0.18) SHDI**			**5**	**-66.32**	**143.81**	**0**	**0.39**	0.03	0.04
	700	Int.	+ Crop				+ (-0.49±0.16) SHDI			9	-61.58	144.98	1.17	0.22	0.03	0.02
	700	Int.			+ (0.18±0.16) PAR		+ (-0.52±0.18) SHDI			6	-65.73	145.14	1.33	0.2	0.03	0.02
	700	Int.	+ Crop		+ (0.27±0.16) PAR		+ (-0.50±0.15) SHDI			10	-60.18	145.14	1.33	0.2	0.03	0.02
	800	**Int.**					**+ (-0.72±0.22) SHDI**			**5**	**-65.58**	**142.34**	**0**	**0.68**	0.62	0.09
	800	Int.			+ (0.17±0.16) PAR		+ (-0.71±0.21) SHDI			6	-65.08	143.85	1.51	0.32	0.62	0.04
	900	**Int.**					**+ (-0.85±0.25) SHDI**			**5**	**-65.36**	**141.90**	**0**	**0.56**	0.08	0.11
	900	Int.		+ Mgmt			+ (-0.85±0.25) SHDI			6	-65	143.68	1.78	0.23	0.08	0.04
	900	Int.			+ (0.13±0.17) PAR		+ (-0.85±0.25) SHDI			6	-65.07	143.82	1.92	0.21	0.08	0.04
	1000	**Int.**					**+ (-0.93±0.29) SHDI**			**5**	**-65.94**	**143.06**	**0**	**0.7**	0.18	0.06
	1000	Int.		+ Mgmt			+ (-0.94±0.29) SHDI			6	-65.53	144.75	1.69	0.3	0.18	0.03

Response	Scale	Model							df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
j) Staphylinid	**100**	**Int.**	**+ Crop**						**8**	**-45.34**	**109.68**	**0**	**0.3**	0.02	0.00
richness	100	Int.							4	-50.64	110.05	0.37	0.25	0.02	0.00
	100	Int.	+ Crop			+ (0.09±0.06) PSH			9	-44.38	110.60	0.92	0.19	0.02	0.00
	100	Int.	+ Crop				+ (-0.11±0.10) SHDI		9	-44.76	111.36	1.68	0.13	0.02	0.00
	100	Int.	+ Crop		+ (0.07±0.07) PAR				9	-44.85	111.53	1.85	0.12	0.02	0.00
	200	**Int.**	**+ Crop**						**8**	**-45.34**	**109.68**	**0**	**0.37**	0.00	0.00
	200	Int.							4	-50.64	110.05	0.37	0.31	0.00	0.00
	200	Int.	+ Crop			+ (0.09±0.08) PSH			9	-44.63	111.09	1.41	0.18	0.00	0.00
	200	Int.	+ Crop				+ (-0.11±0.11) SHDI		9	-44.91	111.65	1.97	0.14	0.00	0.00
	300	**Int.**	**+ Crop**				**+ (-0.21±0.11) SHDI**		**9**	**-43.69**	**109.21**	**0**	**0.2**	0.00	0.00
	300	Int.	+ Crop						8	-45.34	109.68	0.47	0.16	0.00	0.00
	300	Int.	+ Crop		+ (0.16±0.1) PAR		+ (-0.23±0.10) SHDI		10	-42.52	109.81	0.6	0.15	0.00	0.00
	300	Int.							4	-50.64	110.05	0.83	0.13	0.00	0.00
	300	Int.					+ (-0.18±0.12) SHDI		5	-49.66	110.50	1.28	0.1	0.00	0.00
	300	Int.	+ Crop			+ (0.11±0.08) PSH	+ (-0.20±0.10) SHDI		10	-42.9	110.59	1.37	0.1	0.00	0.00
	300	Int.	+ Crop			+ (0.12±0.09) PSH			9	-44.5	110.82	1.61	0.09	0.00	0.00
	300	Int.	+ Crop		+ (0.13±0.11) PAR				9	-44.67	111.17	1.96	0.07	0.00	0.00
	➡ **400**	**Int.**	**+ Crop**		**+ (0.26±0.10) PAR**		**+ (-0.33±0.08) SHDI**		**10**	**-38.42**	**101.62**	**0**	**0.69**	0.00	0.14
	400	Int.	+ Crop		+ (0.23±0.09) PAR	+ (0.10±0.08) PSH	+ (-0.33±0.08) SHDI		11	-37.67	103.22	1.59	0.31	0.00	0.06
	500	**Int.**	**+ Crop**		**+ (0.24±0.09) PAR**	**+ (0.15±0.08) PSH**	**+ (-0.34±0.08) SHDI**		**11**	**-37.28**	**102.44**	**0**	**0.51**	0.04	0.10
	500	Int.	+ Crop		+ (0.25±0.10) PAR		+ (-0.33±0.09) SHDI		10	-38.88	102.54	0.11	0.49	0.04	0.09
	600	**Int.**	**+ Crop**		**+ (0.22±0.09) PAR**	**+ (0.18±0.08) PSH**	**+ (-0.38±0.09) SHDI**		**11**	**-37.42**	**102.71**	**0**	**0.45**	0.06	0.08
	600	Int.	+ Crop		+ (0.24±0.11) PAR		+ (-0.34±0.10) SHDI		10	-39.26	103.29	0.59	0.34	0.06	0.06
	600	Int.	+ Crop			+ (0.20±0.10) PSH	+ (-0.37±0.10) SHDI		10	-39.71	104.20	1.49	0.21	0.06	0.04
	700	**Int.**	**+ Crop**		**+ (0.22±0.12) PAR**		**+ (-0.37±0.11) SHDI**		**10**	**-39.87**	**104.52**	**0**	**0.28**	0.06	0.03
	700	Int.	+ Crop				+ (-0.36±0.12) SHDI		9	-41.56	104.95	0.44	0.22	0.06	0.03
	700	Int.	+ Crop			+ (0.18±0.11) PSH	+ (-0.40±0.12) SHDI		10	-40.28	105.34	0.82	0.18	0.06	0.02
	700	Int.					+ (-0.39±0.14) SHDI		5	-47.22	105.61	1.1	0.16	0.06	0.02
	700	Int.	+ Crop		+ (0.19±0.11) PAR	+ (0.15±0.10) PSH	+ (-0.40±0.11) SHDI		11	-38.87	105.61	1.1	0.16	0.06	0.02
	800	**Int.**					**+ (-0.51±0.17) SHDI**		**5**	**-46.73**	**104.63**	**0**	**0.25**	0.45	0.03
	800	Int.	+ Crop				+ (-0.44±0.15) SHDI		9	-41.72	105.27	0.64	0.18	0.45	0.02
	800	Int.	+ Crop		+ (0.22±0.13) PAR		+ (-0.47±0.14) SHDI		10	-40.35	105.49	0.86	0.16	0.45	0.02
	800	Int.	+ Crop			+ (0.19±0.11) PSH	+ (-0.47±0.14) SHDI		10	-40.45	105.68	1.04	0.15	0.45	0.02
	800	Int.			+ (0.14±0.13) PAR		+ (-0.51±0.17) SHDI		6	-46.11	105.91	1.27	0.13	0.45	0.02
	800	Int.				+ (0.14±0.13) PSH	+ (-0.52±0.16) SHDI		6	-46.18	106.04	1.41	0.12	0.45	0.02
	900	**Int.**					**+ (-0.61±0.20) SHDI**		**5**	**-46.65**	**104.47**	**0**	**0.32**	0.15	0.03
	900	Int.	+ Crop				+ (-0.53±0.18) SHDI		9	-41.91	105.65	1.19	0.18	0.15	0.02
	900	Int.	+ Crop			+ (0.22±0.13) PSH	+ (-0.55±0.17) SHDI		10	-40.71	106.19	1.72	0.13	0.15	0.01
	900	Int.			+ (0.11±0.13) PAR		+ (-0.61±0.19) SHDI		6	-46.31	106.30	1.83	0.13	0.15	0.01
	900	Int.				+ (0.12±0.15) PSH	+ (-0.60±0.19) SHDI		6	-46.34	106.36	1.89	0.12	0.15	0.01
	900	Int.	+ Crop	+ Mgmt		+ (0.56±0.18) PSH	+ (-0.61±0.16) SHDI	+ Mgmt:PSH	12	-37.65	106.39	1.92	0.12	0.15	0.01
	1000	**Int.**					**+ (-0.66±0.23) SHDI**		**5**	**-47.1**	**105.39**	**0**	**0.68**	0.21	0.02
	1000	Int.	+ Crop				+ (-0.56±0.22) SHDI		9	-42.54	106.91	1.52	0.32	0.21	0.01

Response	Scale	Model	df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
k) Spider	**100**	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**0.7**	0.06	0.08
abundance	100	Int. + Crop + (-0.13±0.13) PSH	9	-84.7	191.23	1.73	0.3	0.06	0.03
	200	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**1**	0.02	0.08
	300	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**1**	0.02	0.08
	400	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**1**	0.04	0.08
	500	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**0.73**	0.06	0.08
	500	Int. + Crop + (-0.2±0.22) SHDI	9	-84.83	191.49	1.99	0.27	0.06	0.03
	600	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**1**	0.08	0.08
	700	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**1**	0.13	0.08
	800	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**0.73**	0.22	0.08
	800	Int. + Crop + (-0.27±0.29) PAR	9	-84.81	191.44	1.95	0.27	0.22	0.03
	900	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**0.7**	0.18	0.08
	900	Int. + Crop + (-0.34±0.31) PAR	9	-84.66	191.14	1.65	0.3	0.18	0.04
	➡ **1000**	**Int. + Crop**	**8**	**-85.25**	**189.49**	**0**	**0.65**	0.19	0.08
	1000	Int. + Crop + (-0.42±0.33) PAR	9	-84.45	190.72	1.23	0.35	0.19	0.04

Response	Scale	Model	df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
l) Bird	**100**	**Int.**	**4**	**-51.53**	**111.97**	**0**	**0.3**	0.03	0.00
abundance	100	Int. + Crop	7	-47.88	112.48	0.52	0.23	0.03	0.00
	100	Int. + (0.17±0.14) SHDI	5	-50.84	113.08	1.12	0.17	0.03	0.00
	100	Int. + (-0.13±0.11) PSH	5	-50.93	113.25	1.28	0.16	0.03	0.00
	100	Int. + Crop + (0.16±0.12) SHDI	8	-46.97	113.55	1.58	0.14	0.03	0.00
	200	**Int. + Crop + Mgmt + (0.49±0.12) SHDI + Mgmt:SHDI**	**10**	**-40.27**	**106.33**	**0**	**1**	0.00	0.03
	300	**Int. + Crop + Mgmt + (0.59±0.13) SHDI + Mgmt:SHDI**	**10**	**-39.13**	**104.04**	**0**	**1**	0.01	0.10
	400	**Int. + Crop + (0.41±0.12) SHDI**	**8**	**-43.14**	**105.88**	**0**	**0.56**	0.03	0.04
	400	Int. + Crop + Mgmt + (0.58±0.14) SHDI + Mgmt:SHDI	10	-40.31	106.40	0.52	0.44	0.03	0.03
	500	**Int. + Crop + (0.50±0.13) SHDI**	**8**	**-42.16**	**103.92**	**0**	**1**	0.05	0.10
	600	**Int. + Crop + (0.51±0.14) SHDI**	**8**	**-42.34**	**104.27**	**0**	**1**	0.06	0.09
	700	**Int. + Crop + (0.56±0.15) SHDI**	**8**	**-41.96**	**103.51**	**0**	**1**	0.10	0.13
	➡ **800**	**Int. + Crop + (0.77±0.19) SHDI**	**8**	**-40.98**	**101.56**	**0**	**1**	0.40	0.33
	900	**Int. + Crop + (0.94±0.25) SHDI**	**8**	**-41.91**	**103.42**	**0**	**1**	0.12	0.13
	1000	**Int. + Crop + (0.96±0.30) SHDI**	**8**	**-43.59**	**106.78**	**0**	**1**	0.20	0.02

Response	Scale	Model									df	logLik	AICc	ΔAICc	Weight per scale	Weight across scales (full models)	Weight across scales (final models)
m) Bird	**100**	**Int.**	**+ Crop**	**+ Mgmt**		**+ (0.40±0.12) PSH**			**+ Mgmt:PSH**		**10**	**-14.17**	**54.13**	**0**	**0.44**	0.00	0.00
richness	100	Int.	+ Crop	+ Mgmt		+ (0.39±0.11) PSH	+ (0.14±0.06) SHDI		+ Mgmt:PSH	+ Mgmt:SHDI	12	-11.15	54.97	0.84	0.29	0.00	0.00
	100	Int.	+ Crop	+ Mgmt	+ (0.05±0.03) PAR	+ (0.40±0.11) PSH			+ Mgmt:PSH		11	-13.03	55.19	1.06	0.26	0.00	0.00
	200	**Int.**	**+ Crop**	**+ Mgmt**		**+ (0.25±0.08) PSH**	**+ (0.26±0.06) SHDI**		**+ Mgmt:PSH**	**+ Mgmt:SHDI**	**12**	**-5.52**	**43.70**	**0**	**0.69**	0.00	0.57
	200	Int.	+ Crop	+ Mgmt	+ (0.06±0.04) PAR	+ (0.23±0.08) PSH	+ (0.24±0.06) SHDI		+ Mgmt:PSH	+ Mgmt:SHDI	13	-4.47	45.33	1.63	0.31	0.00	0.25
	300	**Int.**	**+ Crop**	**+ Mgmt**			**+ (0.28±0.08) SHDI**			**+ Mgmt:SHDI**	**10**	**-13.1**	**51.99**	**0**	**0.43**	0.00	0.01
	300	Int.	+ Crop	+ Mgmt		+ (0.10±0.05) PSH	+ (0.30±0.07) SHDI			+ Mgmt:SHDI	11	-11.71	52.55	0.57	0.33	0.00	0.01
	300	Int.	+ Crop	+ Mgmt	+ (0.07±0.04) PAR		+ (0.28±0.07) SHDI			+ Mgmt:SHDI	11	-12.03	53.19	1.2	0.24	0.00	0.00
	400	**Int.**	**+ Crop**	**+ Mgmt**	**+ (0.74±0.20) PAR**			**+ Mgmt:PAR**			**10**	**-13.68**	**53.15**	**0**	**0.57**	0.00	0.01
	400	Int.		+ Mgmt	+ (0.89±0.24) PAR			+ Mgmt:PAR			7	-18.47	53.68	0.53	0.43	0.00	0.00
	500	**Int.**		**+ Mgmt**	**+ (1.04±0.24) PAR**			**+ Mgmt:PAR**			**7**	**-17.57**	**51.88**	**0**	**1**	0.00	0.01
	600	**Int.**		**+ Mgmt**	**+ (1.06±0.22) PAR**			**+ Mgmt:PAR**			**7**	**-16.51**	**49.74**	**0**	**0.51**	0.00	0.03
	600	Int.		+ Mgmt	+ (1.08±0.20) PAR		+ (0.16±0.09) SHDI	+ Mgmt:PAR		+ Mgmt:SHDI	9	-14.14	50.90	1.16	0.29	0.00	0.02
	600	Int.		+ Mgmt	+ (1.14±0.22) PAR	+ (-0.07±0.06) PSH		+ Mgmt:PAR			8	-16	51.59	1.85	0.2	0.00	0.01
	700	**Int.**		**+ Mgmt**	**+ (1.06±0.19) PAR**		**+ (0.24±0.10) SHDI**	**+ Mgmt:PAR**		**+ Mgmt:SHDI**	**9**	**-13.98**	**50.57**	**0**	**0.37**	0.00	0.02
	700	Int.		+ Mgmt	+ (1.00±0.22) PAR			+ Mgmt:PAR			7	-17.07	50.88	0.31	0.32	0.00	0.02
	700	Int.		+ Mgmt	+ (1.02±0.21) PAR		+ (0.11±0.09) SHDI	+ Mgmt:PAR			8	-16.35	52.31	1.74	0.16	0.00	0.01
	700	Int.		+ Mgmt	+ (1.13±0.23) PAR	+ (-0.10±0.08) PSH		+ Mgmt:PAR			8	-16.41	52.42	1.85	0.15	0.00	0.01
	➡ **800**	**Int.**		**+ Mgmt**	**+ (0.97±0.19) PAR**		**+ (0.38±0.13) SHDI**	**+ Mgmt:PAR**		**+ Mgmt:SHDI**	**9**	**-14.36**	**51.34**	**0**	**0.53**	1.00	0.01
	800	Int.		+ Mgmt	+ (0.90±0.22) PAR			+ Mgmt:PAR			7	-18.07	52.87	1.53	0.25	1.00	0.01
	800	Int.		+ Mgmt	+ (0.94±0.21) PAR		+ (0.20±0.12) SHDI	+ Mgmt:PAR			8	-16.76	53.11	1.77	0.22	1.00	0.01
	900	**Int.**		**+ Mgmt**	**+ (1.01±0.22) PAR**		**+ (0.52±0.19) SHDI**	**+ Mgmt:PAR**		**+ Mgmt:SHDI**	**9**	**-16.05**	**54.71**	**0**	**0.4**	0.00	0.00
	900	Int.		+ Mgmt	+ (0.83±0.24) PAR			+ Mgmt:PAR			7	-19.41	55.55	0.85	0.26	0.00	0.00
	900	Int.	+ Crop	+ Mgmt			+ (0.35±0.16) SHDI				9	-16.76	56.14	1.44	0.19	0.00	0.00
	900	Int.		+ Mgmt	+ (0.90±0.24) PAR		+ (0.23±0.17) SHDI	+ Mgmt:PAR			8	-18.51	56.61	1.91	0.15	0.00	0.00
	1000	**Int.**	**+ Crop**	**+ Mgmt**							**8**	**-18.8**	**57.20**	**0**	**0.13**	0.00	0.00
	1000	Int.									4	-24.23	57.38	0.17	0.12	0.00	0.00
	1000	Int.				+ (0.27±0.18) PSH					5	-23.17	57.73	0.52	0.1	0.00	0.00
	1000	Int.	+ Crop								7	-20.65	58.04	0.83	0.09	0.00	0.00
	1000	Int.	+ Crop			+ (0.27±0.15) PSH					8	-19.31	58.23	1.02	0.08	0.00	0.00
	1000	Int.	+ Crop			+ (0.32±0.14) PSH	+ (0.38±0.21) SHDI				9	-17.85	58.31	1.11	0.08	0.00	0.00
	1000	Int.	+ Crop	+ Mgmt			+ (0.27±0.21) SHDI				9	-17.97	58.55	1.34	0.07	0.00	0.00
	1000	Int.		+ Mgmt	+ (0.73±0.28) PAR			+ Mgmt:PAR			7	-20.92	58.57	1.37	0.07	0.00	0.00
	1000	Int.			+ (0.17±0.15) PAR						5	-23.61	58.61	1.4	0.07	0.00	0.00
	1000	Int.	+ Crop	+ Mgmt		+ (0.19±0.15) PSH					9	-18.02	58.65	1.44	0.07	0.00	0.00
	1000	Int.		+ Mgmt							5	-23.65	58.70	1.5	0.06	0.00	0.00
	1000	Int.	+ Crop	+ Mgmt		+ (0.24±0.14) PSH	+ (0.36±0.20) SHDI				10	-16.51	58.81	1.61	0.06	0.00	0.00

4.8. Supplementary Figures

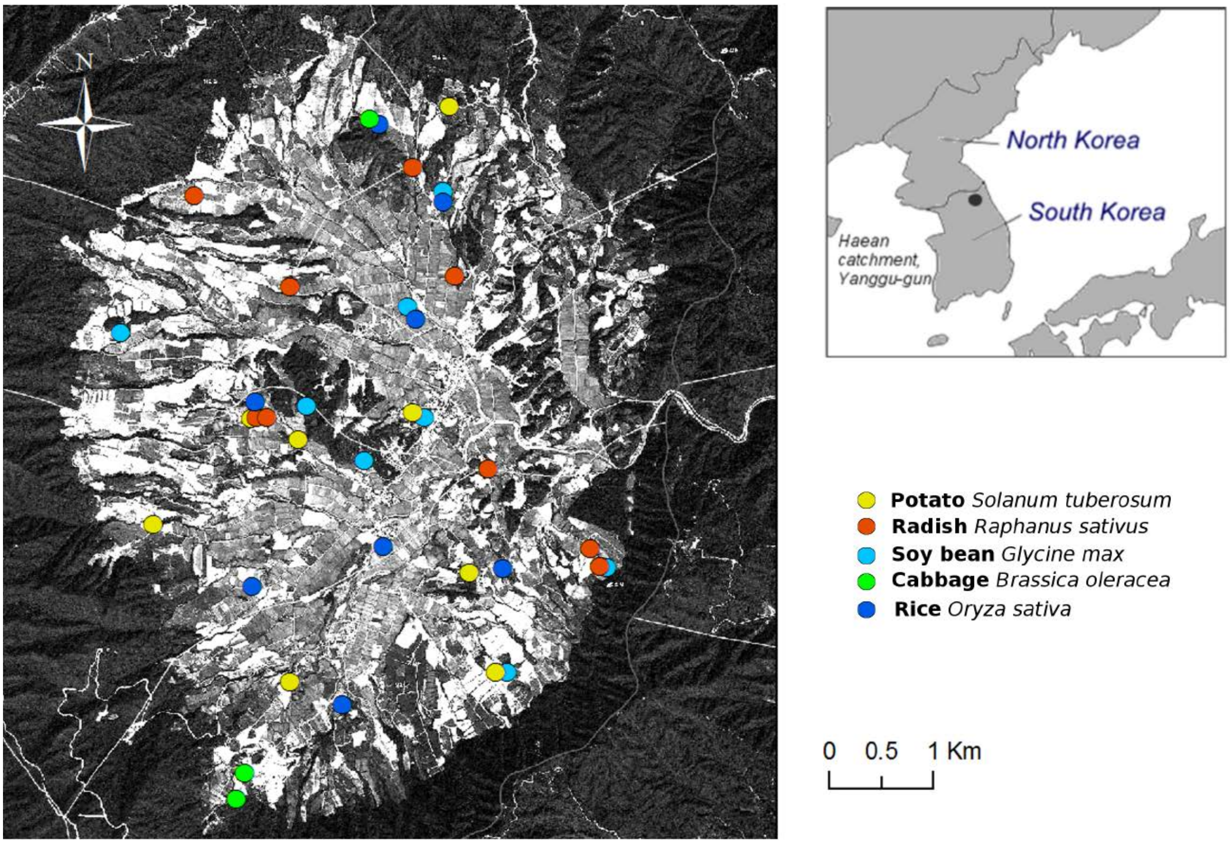

Figure S 4.1. Map of the Haean catchment and location of sampling plots. Satellite image modified from Cnes/Spot Image (Google Maps ©2013).

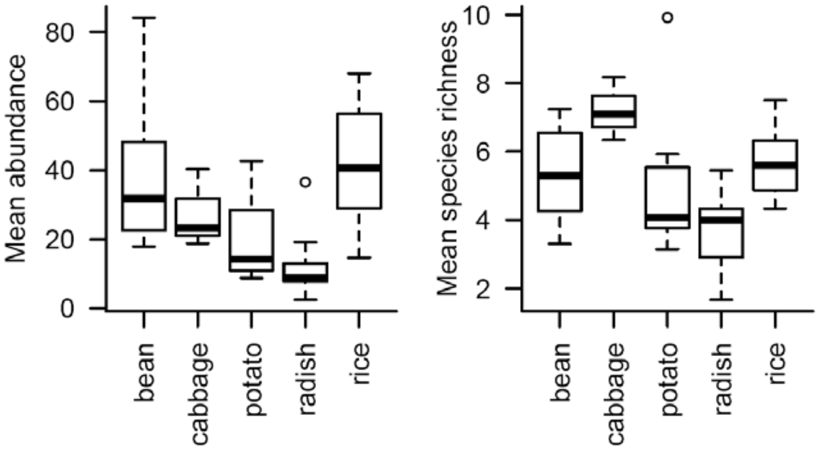

Figure S 4.2. Mean overall abundance (a) and species richness (b) of focal taxa in 5 sampled crop types.

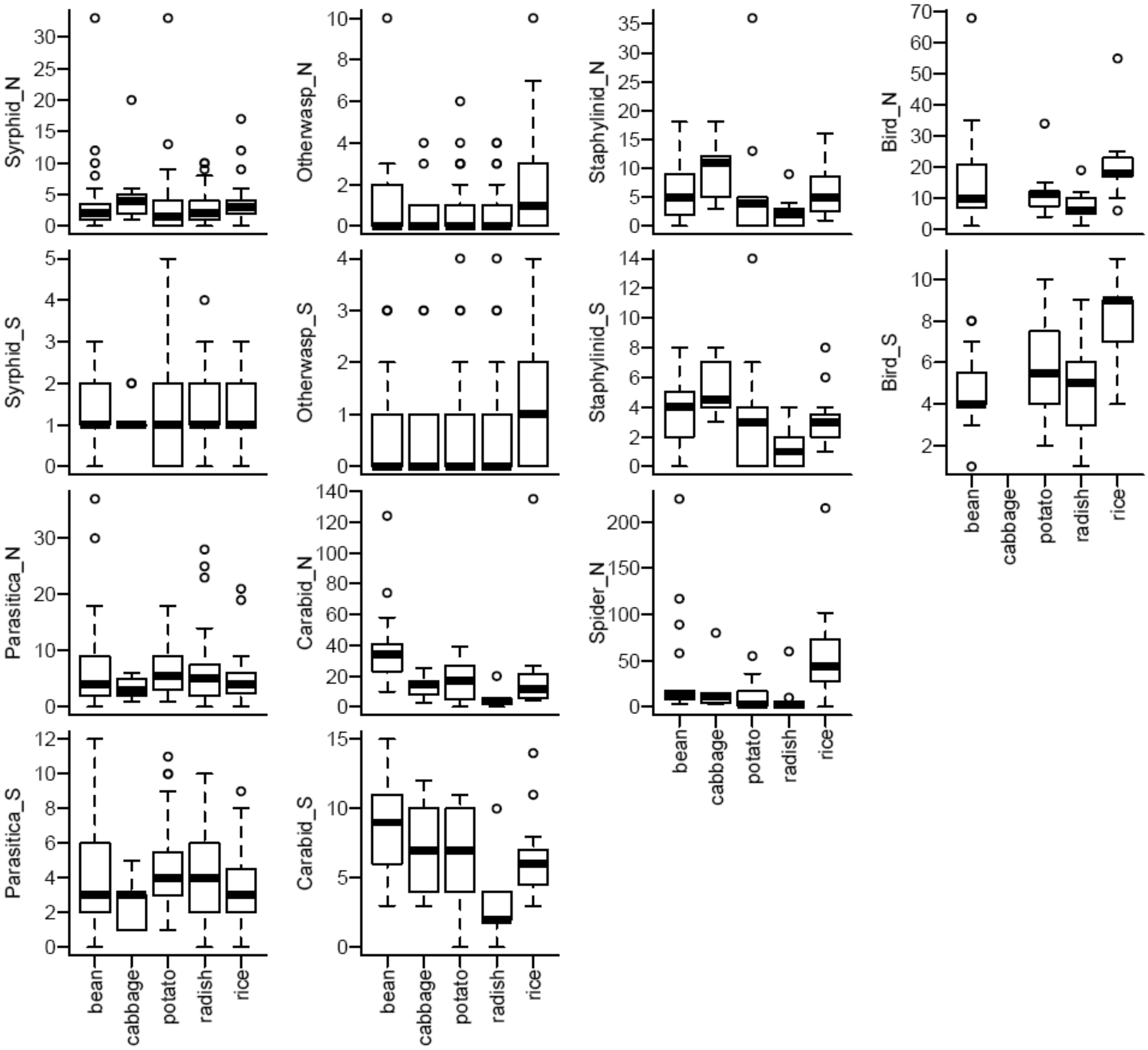

Figure S 4.3. Abundance (N) and species richness (S) of focal taxa in 5 sampled crop types.

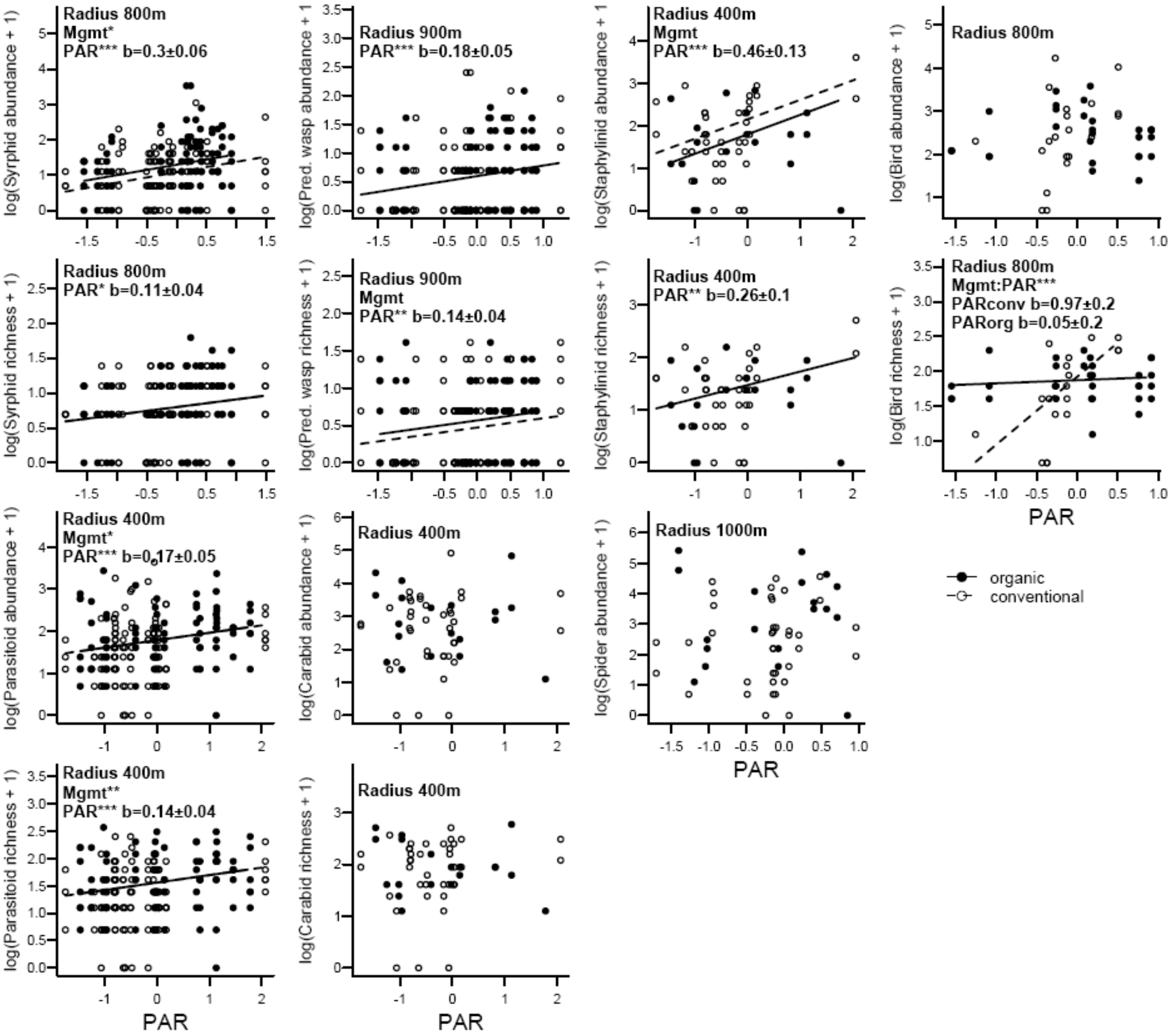

Figure S 4.4. Effects of landscape configuration (perimeter-area ratio ‘PAR’) and management intensity (organic vs. conventional, ‘Mgmt’) on the abundance and species richness of natural enemy groups. Graphs are shown at the most predictive scales selected for each response variable. Regression lines represent predicted values of linear mixed effects models at the chosen scale. Full points and solid lines: organic, open points and dashed lines: conventional management.

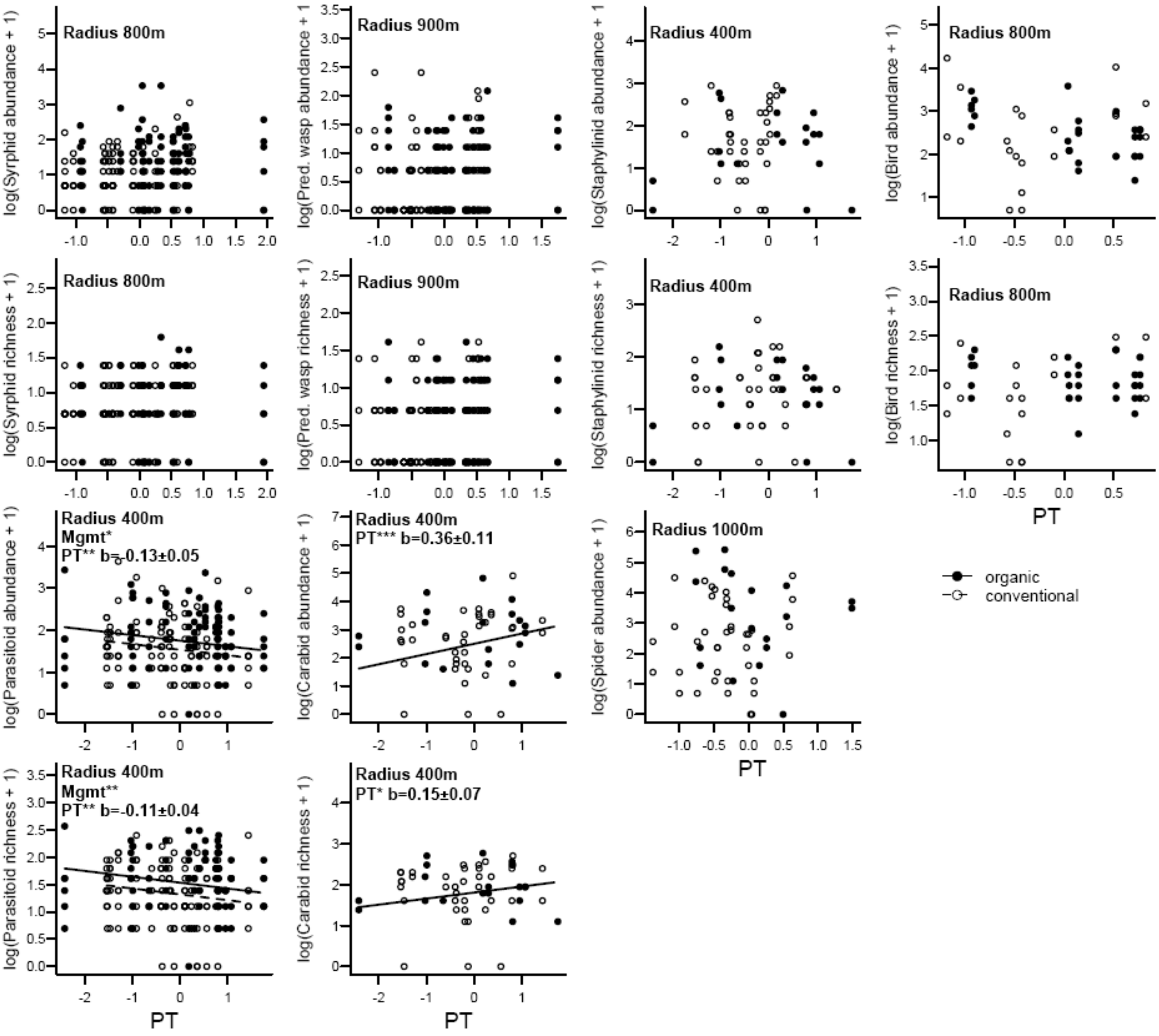

Figure S 4.5. Effects of landscape composition (% seminatural habitat ‘PSH’) and management intensity (organic vs. conventional, ‘Mgmt’) on the abundance and species richness of natural enemy groups. Graphs are shown at the most predictive scales selected for each response variable. Regression lines represent predicted values of linear mixed effects models at the chosen scale. Full points and solid lines: organic, open points and dashed lines: conventional management.

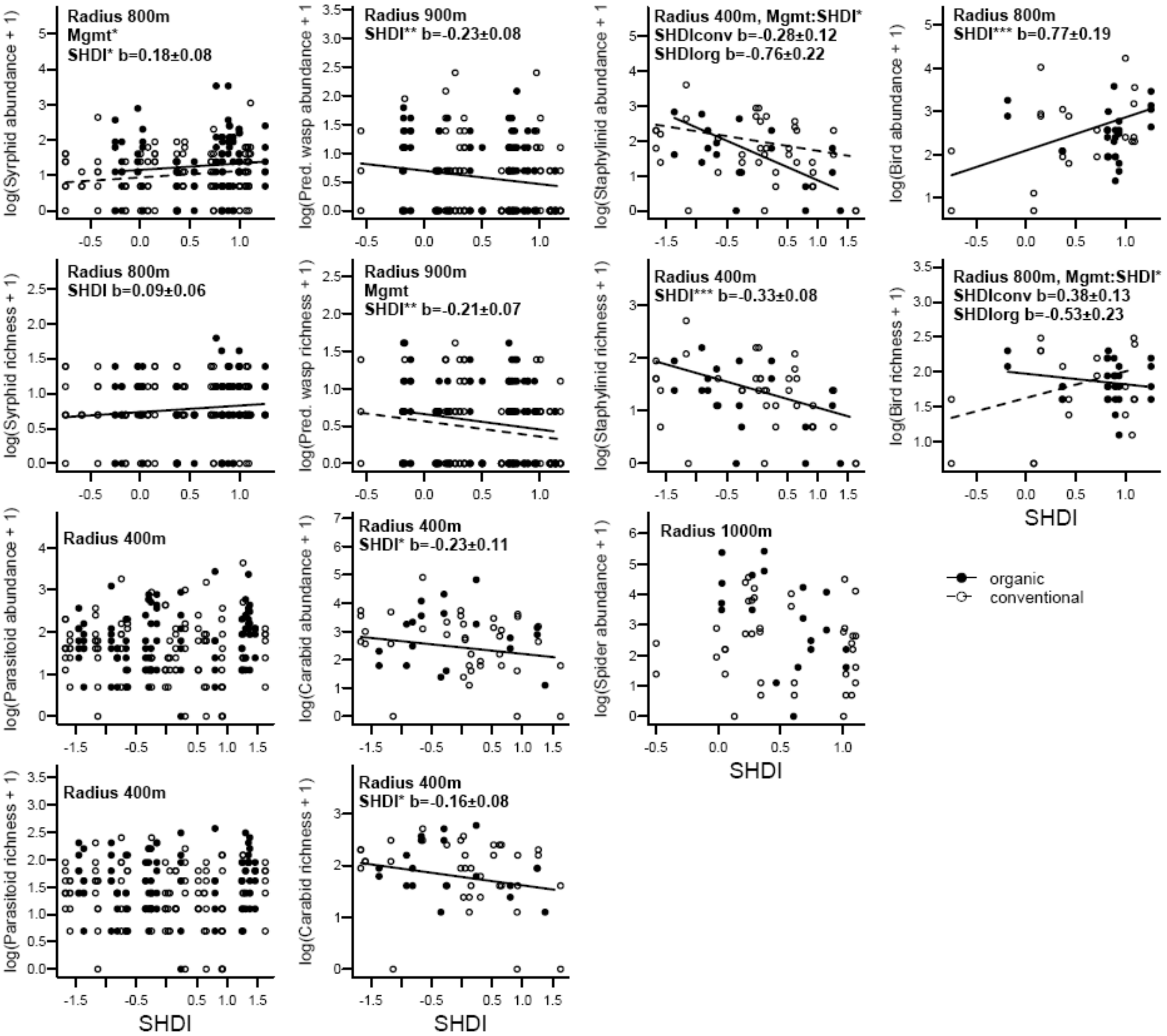

Figure S 4.6. Effects of landscape diversity (Shannon´s index of habitat diversity ‘SHDI’) and management intensity (organic vs. conventional, ‘Mgmt’) on the abundance and species richness of natural enemy groups. Graphs are shown at the most predictive scales selected for each response variable. Regression lines represent predicted values of linear mixed effects models at the chosen scale. Full points and solid lines: organic, open points and dashed lines: conventional management.

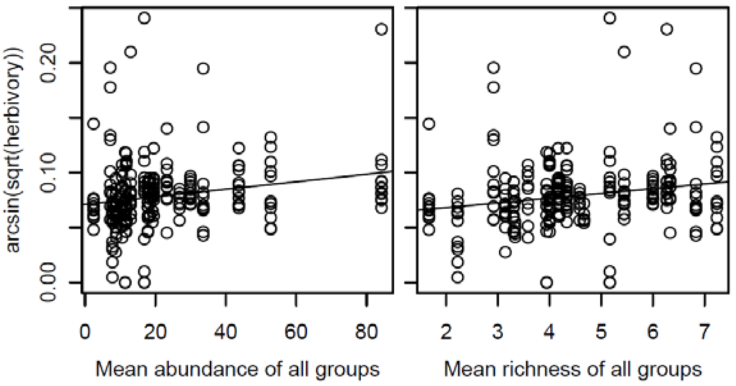

Figure S 4.7. Relationship between crop herbivory (arcsine-square root transformed) and mean overall abundance (a) and richness (b) of natural enemy groups.

4.9. Appendix to chapter 4

Appendix 4.1. List of species sampled in focal crop fields of the Haean catchment, South Korea.

Identification level	Sampling method	Enemy group	Taxonomic group	Species (morphospecies) or family	Total abundance	Function
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Chalcosyrphus latifrons* (Shiraki & Edashige, 1953)	2	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Cheilosia* sp. 1 (Meigen, 1838)	2	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Eristalis arbustorum* (Linnaeus, 1758)	14	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Eristalis cerealis* (Fabricius, 1805)	2	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Eristalis tenax* (Linnaeus, 1758)	26	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Helophilus virgatus* (Coquillett, 1898)	1	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Mesembrius flaviceps* (Matsumura ,1905)	4	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Mesembrius niger* (Shiraki, 1968)	2	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Syritta pipiens* (Linnaeus, 1758)	9	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Xylota abiens* (Meigen, 1822)	8	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Xylota coquilletti* (Hervé-Bazin, 1914)	11	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Xylota* sp.1 (Meigen, 1822)	7	Pollinator*
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Episyrphus balteatus* (De Geer, 1776)	377	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Eupeodes corollae* (Fabricius, 1794)	192	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Eupeodes nitens* (Zetterstedt, 1843)	3	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Melanostoma mellinum* (Linnaeus, 1758)	20	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Sphaerophoria indiana* (Bigot, 1884)	28	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Sphaerophoria menthastri* (Vockeroth, 1963)	22	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Sphaerophoria rueppellii* (Weidemann, 1820)	2	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Syrphus torvus* (Osten Sacken, 1875)	1	Pollinator/predator
species	Pan trap	Syrphid (hover) flies	Syrphidae	*Triglyphus primus* (Loew, 1840)	1	Pollinator/predator
family	Pan trap	Parasitoid wasps	Parasitica	Aphelinidae	76	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Braconidae	203	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Ceraphronidae	39	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Chalcididae	1	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Chalcidoidea fam.1	10	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Diapriidae	14	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Elasmidae	2	Parasitoid (Lepidoptera, *Polistes*)
family	Pan trap	Parasitoid wasps	Parasitica	Encyrtidae	141	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Eucoilidae	194	Parasitoid (flies)
family	Pan trap	Parasitoid wasps	Parasitica	Eulophidae	62	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Eupelmidae	3	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Eurytomidae	5	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Figitidae	9	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Ichneumonidae	71	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Megaspilidae	18	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Mymaridae	89	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Mymmaromatidae	2	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Perilampidae	11	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Proctotrupidae	4	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Pteromalidae	71	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Scelionidae	128	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Signiphoridae	13	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Torymidae	2	Parasitoid
family	Pan trap	Parasitoid wasps	Parasitica	Trichogrammatidae	23	Parasitoid
family	Pan trap	Gall wasps	Parasitica	Cynipidae	2	Gall wasp*
family	Pan trap	Parasitoid wasps	Parasitica	Ormyridae	2	Parasitoid (gall wasps)
family	Pan trap	Parasitoid wasps	Parasitica	Platygastridae	22	Parasitoid (gall midges)
species	Pan trap	Predatory wasps	Aculeata	*Ammophila sabulosa* (Linnaeus, 1758)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Ancistrocerus japonicus* (Schulthess, 1908)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Campsomeriella annulata* (Fabricius, 1793)	1	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Cerceris hortivaga* (Kohl, 1880)	2	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	Eumeninae sp. 1	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Euodynerus nipanicus* (Giordani Soika, 1995)	1	Predator
family	Pan trap	Predatory wasps	Aculeata	Formicidae spp.	22	Predator
species	Pan trap	Predatory wasps	Aculeata	*Larra carbonaria* (Smith, 1858)	1	Parasitoid (crickets)
species	Pan trap	Predatory wasps	Aculeata	*Liris festinans* (Smith, 1858)	1	Parasitoid (crickets)
species	Pan trap	Predatory wasps	Aculeata	*Nysson spinosus* (Forster, 1771)	1	Parasitoid (*Argogorytes* wasps)
species	Pan trap	Predatory wasps	Aculeata	*Oxybelus* sp. 1 (Latreille, 1797)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Pemphredon* sp. 1 (Latreille, 1796)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Polistes snelleni* (Saussure, 1862)	1	Predator
family	Pan trap	Predatory wasps	Aculeata	Pompilidae spp.	12	Predator (spiders)
subfamily	Pan trap	Predatory wasps	Aculeata	Pompilinae spp.	12	Predator (spiders)
family	Pan trap	Predatory wasps	Aculeata	Sphecidae spp.	38	Predator
species	Pan trap	Predatory wasps	Aculeata	*Tiphia agilis* (Smith, 1873)	37	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia latistriata* (Allen & Jaynes, 1930)	3	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia malayana* (Cameron, 1910)	2	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia ordinaria* (Smith, 1873)	8	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia popilliavora* (Rohwer, 1924)	40	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia rufomandibulata* (Smith, 1875)	3	Parasitoid (beetles)

Appendix 4.1 (continued)

Identification level	Sampling method	Enemy group	Taxonomic group	Species (morphospecies) or family	Total abundance	Function
species	Pan trap	Predatory wasps	Aculeata	*Tiphia* sp. 1 (Fabricius, 1775)	11	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Tiphia sternocarinata* (Allen & Jaynes, 1930)	1	Parasitoid (beetles)
species	Pan trap	Predatory wasps	Aculeata	*Trichrysis cyanea* (Linnaeus, 1758)	1	Parasitoid (*Trypoxylon* wasps)
species	Pan trap	Predatory wasps	Aculeata	*Trypoxylon fronticorne japonense* (Tsuneki,	1	Predator (spiders)
species	Pan trap	Predatory wasps	Aculeata	*Trypoxylon koma* (Tsuneki, 1956)	10	Predator (spiders)
species	Pan trap	Predatory wasps	Aculeata	*Vespula flaviceps* (Smith, 1870)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Vespula koreensis* (Radoszkowski, 1887)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	*Vespula shidai* (Ish.,Yam.,Wagn., 1980)	1	Predator
species	Pan trap	Predatory wasps	Aculeata	Aculeata sp.1	1	Predator†
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Agonum* sp. 1 (cf. *Atricomes*) (Bates, 1873)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Amara congrua* (Morawitz, 1862)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Amara gigantea* (Motschulsky, 1844)	5	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Amara majuscula* (Chaudoir, 1850)	3	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Amara sinuaticollis* (Morawitz, 1862)	2	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Anisodactylus punctatipennis* (Morawitz,1862)	28	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Anisodactylus signatus* (Panzer, 1796)	51	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Archipatrobus femoralis femoralis* (Motschulsky, 1864)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Bembidion scopulinum* (Kirby, 1837)	40	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Bembidion* sp. 1 (Latreille, 1802)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	Carabidae sp. 1	19	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Carabus koreanus* (Reitter, 1895)	3	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Carabus smaragdinus* (Fischer-Waldheim, 1823 sensu lato)	5	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Carabus tuberculosus* (Dejean, 1829)	7	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius inops inops* (Chaudoir, 1856)	2	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius micans* (Fabricius, 1792)	45	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius ocreatus* (Bates, 1873)	2	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius pallipes* (Gebler, 1823)	130	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius posticalis* (Motschulsky, 1854)	3	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Chlaenius variicornis* (Morawitz, 1863)	177	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Dicranoncus femoralis* (Chaudoir, 1850)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Dolichus halensis* (Schaller, 1783)	203	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus bungii* (Chaudoir, 1844)	6	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus capito* (Morawitz, 1862)	102	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus chalcentus* (Bates, 1873)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus corporosus* (Motschulsky, 1861)	9	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus eous* (Tschitschérine, 1901)	17	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus griseus* (Panzer, 1796)	29	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus jureceki* (Jedlicka, 1928)	27	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus modestus* (Dejean, 1829)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus pastor pastor* (Motschulsky, 1844)	43	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus sinensis* (Ochs, 1924)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus sinicus* (Hope, 1845)	21	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus* sp. 1 (Latreille, 1802)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus* sp. 2 (Latreille, 1802)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus tridens* (Morawitz, 1862)	102	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Harpalus ussuriensis ussuriensis* (Chaudoir, 1863)	32	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Nebria chinensis* (Bates, 1872)	6	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Nebria coreica* (Solsky, 1875)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Nipponoharpalus discrepans* (Morawitz, 1862)	16	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pheropsophus jessoensis* (Morawitz, 1862)	3	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	Platynini sp. 1	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Poecilus nitidicollis nitidicollis* (Motschulsky, 1844)	16	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pristosia nitidula* (Morawitz, 1862)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pristosia proxima* (Morawitz, 1862)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pterostichus haptoderoides haptoderoides* (Tschitschérine, 1889)	6	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pterostichus microcephalus* (Motschulsky, 1860)	12	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pterostichus scurra (*Tschitschérine, 1901)	2	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pterostichus subovatus subovatus* (Motschulsky, 1860)	3	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Pterostichus sulcitarsis* (Morawitz, 1862)	16	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Sphaerotachys* cf. *laetificus* (Bates, 1873)	33	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Stenolophus difficilis* (Hope, 1845)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Stenolophus propinquus* (Morawitz, 1862)	4	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Synuchus agonus* (Tschitschérine, 1895)	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Synuchus orbicollis* (A. Morawitz, 1862)	6	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	Tachyini sp. 1	1	Predator
species	Pitfall (funnel) trap	Carabid (ground) beetles	Carabidae	*Trigonognatha coreana* (Tschitschérine, 1895)	2	Predator

Appendix 4.1 (continued)

Identification level	Sampling method	Enemy group	Taxonomic group	Species (morphospecies) or family	Total abundance	Function
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Acrotona* sp. 1 (Thomson, 1859)	25	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Acrotona* sp. 2 (Thomson, 1859)	5	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Acrotona* sp. 3 (Thomson, 1859)	14	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Aleochara (Aleochara) curtula* (Goeze, 1777)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Aleochara (Coprochara) verna* (Say, 1836)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Algon sphaericollis* (Schillhammer, 2006)	10	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Aloconota* sp. 1 (Thomson, 1858)	3	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Amischa* sp. 1 (Thomson, 1859)	9	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Anotylus* sp. 1 (Thomson, 1859)	7	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Atheta (Microdota) koreana* (Bernhauer, 1922)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Atheta* sp. 1 (Thomson, 1858)	21	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Atheta* sp. 2 (Thomson, 1858)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Atheta* sp. 3 (Thomson, 1858)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Carpelimus* sp. 1 (Kirby, 1819)	22	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Carpelimus* sp. 2 (Kirby, 1819)	12	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Carpelimus* sp. 3 (Kirby, 1819)	4	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Euconnus* sp. 1 (Thomson, 1859)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Falagria caesa (* Erichson, 1839)	38	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Lathrobium* sp. 1 (Gravenhorst, 1802)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Lathrobium* sp. 2 (Gravenhorst, 1802)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Lithocharis nigriceps* (Kraatz, 1859)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Nehemitropia lividipennis* (Mannerheim, 1830)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Nehemitropia* sp. 1 (Lohse, 1971)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Neobisnius inornatus* (Sharp,1889)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Ocypus* sp. 1 (Leach, 1819)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Ocypus* sp. 3 (Leach, 1819)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Oligota* sp. 1 (Mannerheim, 1830)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Oxypoda* sp. 1 (Mannerheim, 1830)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	Oxypodini sp. 1	7	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Paederus parallelus* (Weise, 1877)	3	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Philhygra* sp. 1 (Mulsant & Rey, 1873)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Philonthus (Philonthus) aeneipennis* (Boheman, 1858)	36	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Philonthus (Philonthus) numata* (Dvorák, 1958)	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Philonthus (Philonthus) ohizumi* (Dvorák, 1958)	19	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Platystethus operosus* (Sharp,1874)	42	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Rabigus inconstans* (Sharp, 1889)	10	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Scopaeus (Scopaeus) currax* (Sharp,1889)	12	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Scopaeus* sp. 1 (Erichson, 1840)	9	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Scopaeus* sp. 2 (Erichson, 1840)	4	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	Staphylinidae sp.1	2	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Stenus* sp. 1 (Latreille, 1796)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Stenus* sp. 2 (Latreille, 1796)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Tachinus (Tachinoderus) nigriceps nigriceps* (Sharp, 1888)	1	Predator
species	Pitfall (funnel) trap	Staphylinid (rove) beetles	Staphylinidae	*Zyras pictus* (Sharp, 1874)	6	Predator
order	Pitfall (funnel) trap	Spiders	Araneae	Araneae	1868	Predator
species	Point count	Birds	Aves	*Aix galericulata* (Linnaeus, 1758)	2	Predator
species	Point count	Birds	Aves	*Anas platyrhynchos* (Linnaeus, 1758)	6	Predator
species	Point count	Birds	Aves	*Ardea cinerea* (Linnaeus, 1758)	1	Predator
species	Point count	Birds	Aves	*Egretta alba* (Linnaeus, 1758)	5	Predator
species	Point count	Birds	Aves	*Egretta intermedia* (Wagler, 1827)	5	Predator
species	Point count	Birds	Aves	*Halcyon pileata* (Boddaert, 1783)	10	Predator
species	Point count	Birds	Aves	*Nycticorax nycticorax* (Linnaeus, 1758)	1	Predator
species	Point count	Birds	Aves	*Acrocephalus orientalis* (Temminck & Schlegel, 1847)	12	Predator
species	Point count	Birds	Aves	*Carduelis sinica* (Linnaeus, 1766)	5	Predator
species	Point count	Birds	Aves	*Cettia diphone* (Kittlitz, 1830)	4	Predator
species	Point count	Birds	Aves	*Corvus macrorhynchos* (Wagler, 1827)	26	Predator
species	Point count	Birds	Aves	*Cuculus canorus* (Linnaeus, 1758)	41	Predator
species	Point count	Birds	Aves	*Cuculus poliocephalus* (Latham, 1790)	2	Predator
species	Point count	Birds	Aves	*Cuculus saturatus* (Blyth, 1843)	1	Predator
species	Point count	Birds	Aves	*Cyanopica cyana* (Pallas, 1776)	40	Predator
species	Point count	Birds	Aves	*Dendrocopos kizuki* (Temminck, 1836)	2	Predator
species	Point count	Birds	Aves	*Dendrocopos major* (Linnaeus, 1758)	2	Predator

Appendix 4.1 (continued)

Identification level	Sampling method	Enemy group	Taxonomic group	Species (morphospecies) or family	Total abundance	Function
species	Point count	Birds	Aves	*Emberiza elegans* (Temminck, 1835)	3	Predator
species	Point count	Birds	Aves	*Hirundo rustica* (Linnaeus, 1758)	47	Predator
species	Point count	Birds	Aves	*Hypsipetes amaurotis* (Temminck, 1830)	50	Predator
species	Point count	Birds	Aves	*Lanius bucephalus* (Temminck & Schlegel, 1845)	41	Predator
species	Point count	Birds	Aves	*Lanius cristatus* (Linnaeus, 1758)	4	Predator
species	Point count	Birds	Aves	*Lanius tigrinus* (Drapiez, 1828)	3	Predator
species	Point count	Birds	Aves	*Motacilla alba* (Linnaeus, 1758)	4	Predator
species	Point count	Birds	Aves	*Motacilla cinerea* (Tunstall, 1771)	29	Predator
species	Point count	Birds	Aves	*Oriolus chinensis* (Linnaeus, 1766)	32	Predator
species	Point count	Birds	Aves	*Parus major* (Linnaeus, 1758)	13	Predator
species	Point count	Birds	Aves	*Parus palustris* (Linnaeus, 1758)	1	Predator
species	Point count	Birds	Aves	*Passer montanus* (Linnaeus, 1758)	136	Predator
species	Point count	Birds	Aves	*Phoenicurus auroreus* (Pallas, 1776)	23	Predator
species	Point count	Birds	Aves	*Pica pica* (Linnaeus, 1758)	16	Predator
species	Point count	Birds	Aves	Picidae sp. 1 (Vigors, 1825)	2	Predator
species	Point count	Birds	Aves	*Picus canus* (Gmelin, 1788)	6	Predator
species	Point count	Birds	Aves	*Saxicola torquata* (Linnaeus, 1766)	9	Predator
species	Point count	Birds	Aves	*Streptopelia orientalis* (Latham, 1790)	57	Predator
species	Point count	Birds	Aves	*Sturnus cineraceus* (Temminck, 1835)	5	Predator
species	Point count	Birds	Aves	*Turdus pallidus* (Gmelin, 1789)	2	Predator
species	Point count	Birds	Aves	*Turdus* sp. 1 (Linnaeus, 1758)	1	Predator
species	Point count	Birds	Aves	*Upupa epops* (Linnaeus, 1758)	2	Predator

* Species not included in natural enemy analyses.

† An unidentified Aculeata (not bee) was assumed to be a predator.

Formicidae and unidentified Pompilidae, Pompilinae and Sphecidae were pooled for analysis at (sub)family level.

The function ‘predator’ was assigned to all species known to prey on terrestrial insects at any stage of their life cycle, regularly or occasionally. The function ‘parasitoid’ characterizes species whose larvae develop inside and kill a host. When known and specific, hosts and prey are shown in parentheses. Syrphids whose larvae do not consume other insects (pollinators only) and gall wasps (Cynipidae) were excluded from further analyses.

Part 3

Chapter 5

5. Intraguild predation in a spatial context: the influence of landscape heterogeneity

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Abstract

Intraguild predation (IGP) by top predators on the mesopredators of a shared prey (e.g. herbivores) is ubiquitous across systems. However, few theoretical studies have investigated the outcome of IGP for shared prey across gradients in landscape complexity. Here, using a spatially-explicit model, we show that the impact of IGP on prey when top predators are vertebrates depends on the amount and configuration of habitat in the landscape. In landscapes with high amounts of habitat and low spatial autocorrelation, IGP by vertebrate predators leads to a release of the shared prey from mesopredator pressure, as predicted by theory. However, in landscapes with small amounts of habitat and high autocorrelation, IGP leads to a reduction of the number of prey, despite top predator impacts on mesopredators. This result is explained by differences in the local stability of mesopredator populations across landscapes. When mesopredators are locally unstable, top predators stabilize mesopredator-prey interactions and lead to higher prey consumption than with mesopredators alone. These findings help expand previous IGP theory to spatially explicit systems. They have implications for empirical studies of predator-prey interactions at large spatial scales and for the effective landscape-wide implementation of biological pest control by natural enemies.

Keywords

Trophic network, landscape structure, vertebrate predator, arthropod prey, terrestrial food web, stability, metacommunity, local extinctions

5.1. Introduction

Intraguild predation (IGP) is the ability of a top predator to consume both other predators and a shared prey, and is ubiquitous across terrestrial and aquatic systems (Polis et al., 1989). Several theoretical models have been developed to predict the effects of IGP on populations, communities and resources through the dynamics of food webs and trophic cascades (Polis and Holt, 1992; Polis and Strong, 1996; Holt and Polis, 1997; Holt and Huxel, 2007). According to these predictions, predation by top predators on intermediate predators should lead to an increase in the densities of shared prey, which is not or only partially compensated by direct effects of top predators on the prey (Polis and Holt, 1992; Holt and Polis, 1997). The predicted consequence of such a trophic cascade is a depressed resource for the shared prey, such as a reduced plant biomass caused by increased herbivore pressure.

These predictions are confirmed by empirical studies in terrestrial systems where intermediate and top predators are invertebrates (Vance-Chalcraft et al., 2007). However, they are contradicted by results of terrestrial studies where top predators are vertebrates, preying on assemblages of arthropod predators and prey (Mooney et al., 2010; Mäntylä et al., 2011). In these studies, vertebrate predators are shown to effectively lead to herbivore reduction and increased plant biomass, despite intraguild predation on intermediate predators. This suggests that the consequences of terrestrial vertebrate intraguild predation are not adequately explained by current food web theory (Mooney et al., 2010).

Recently, much interest has been sparked by the recognition that spatial dynamics at landscape scales may play an important role in predator-prey interactions (Amarasekare, 2008; Kissling et al., 2011; Logue et al., 2011). Empirically, a growing body of knowledge shows that spatial heterogeneity of the landscape affects the distribution and abundance of interacting species at scales dependent on body size and mobility (Tscharntke et al., 2012), while species interactions are shown to take place across habitat boundaries (Knight et al., 2005; Casini et al., 2012). Theoretically, the effects on predator-prey interactions of spatial refuges and of spillover between adjacent high- and low-risk habitats are being explored (Abrams et al., 2012). However, in contrast to local heterogeneity (Janssen et al., 2007), few theoretical studies have directly addressed the consequences of large-scale spatial heterogeneity for intraguild predation in structured metacommunities (Amarasekare, 2008; Massol et al., 2011; Casini et al., 2012). In these studies, the mechanisms for stable coexistence of intraguild predators and prey are investigated, including hypotheses of habitat refuges and alternative prey for intraguild predators (Holt and Huxel, 2007; Amarasekare, 2008; Abrams et al., 2012). However, studies investigating the consequences of intraguild predation for the shared prey, under varying conditions of landscape-scale heterogeneity and assuming that species coexist at the landscape scale, are lacking.

In a recent empirical study (Martin et al., 2013), spatial heterogeneity of an agroecosystem is shown to influence the effects of vertebrate intraguild predation. In complex landscapes with large amounts of seminatural habitat, vertebrate top predators (birds) appeared to reduce intermediate predators (wasps) and release the shared prey (pest larvae), in agreement with theoretical predictions, and with previous work on invertebrate top predators (Figure 5.1) (Holt and Polis, 1997; Vance-Chalcraft et al., 2007). However, in simple landscapes, top predators appeared to directly reduce the shared prey, in contrast with theoretical predictions. Intriguingly, similar results in contrast with theory have been found for a range of vertebrate top predator systems (Mooney et al., 2010; Mäntylä et al., 2011), the majority of which were performed in structurally homogeneous, woody or open metaecosystems (but see Floyd, 1996; Mooney et al., 2010; Mäntylä et al., 2011; Massol et al., 2011). Here, we hypothesize that landscape

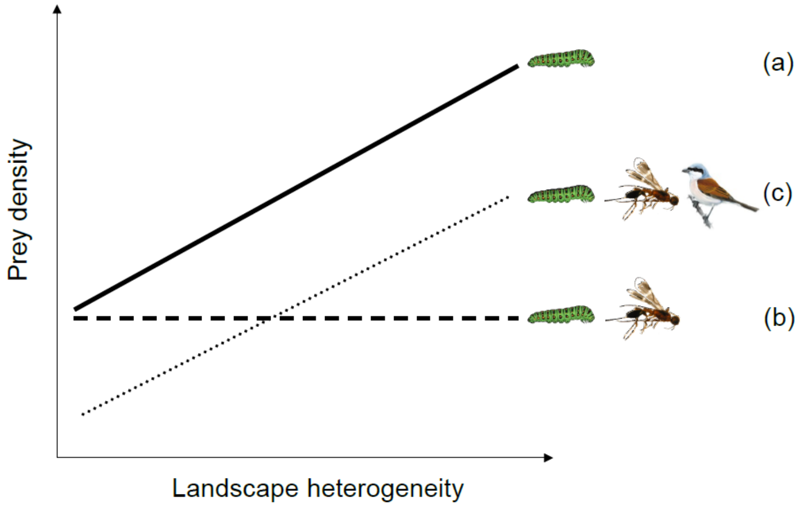

Figure 5.1. Conceptual representation of prey density as a function of landscape heterogeneity (adapted from results of (Martin et al., 2013). (a) Prey density in the absence of predators increases with landscape complexity. (b) In the presence of a mesopredator (wasp), prey density is reduced increasingly strongly with increasing landscape complexity. (c) When a top predator is present, its impact on mesopredators releases the shared prey in complex landscapes, leading to higher prey density than with mesopredators only. However, in simple landscapes, top predators contribute along with mesopredators to reducing the shared prey.

heterogeneity may explain observed differences in the consequences of trophic cascades caused by terrestrial vertebrate or invertebrate top predator systems (Figure 5.1) (Mooney et al., 2010). We thus do not address the causes of species coexistence in heterogeneous systems. Rather, our aim is to clarify the outcome of intraguild predation for the shared (herbivorous) prey across gradients in landscape heterogeneity, assuming that species do coexist in these systems according to previously explored mechanisms of habitat refuges and alternative prey for top predators (Holt and Huxel, 2007; Abrams et al., 2012).

Using the model system of Martin et al. (2013), we thus explore the effects on densities of herbivorous prey of i) no predation, ii) predation by an arthropod mesopredator, and iii) predation by a mesopredator and a vertebrate top predator, itself responsible for intraguild predation of the mesopredator. We consider these effects across a gradient in landscape complexity, in which a landscape is characterized by 1) variable amounts of ‘suitable’ vs. ‘unsuitable’ habitat patches, which determine the quantity of resources available for prey and mesopredators; 2) variable degrees of habitat aggregation or autocorrelation, corresponding to the configurational complexity of the landscape, which determine the accessibility of resources for prey and mesopredators. Based on the model system of (Martin et al., 2013), we assume a scenario of coincidental intraguild predation (Figure 5.2), in which top predators (birds, TP) consume the shared prey (herbivores, H), which may or may not happen to be parasitized by larvae of the mesopredator (parasitoid wasps, MP).

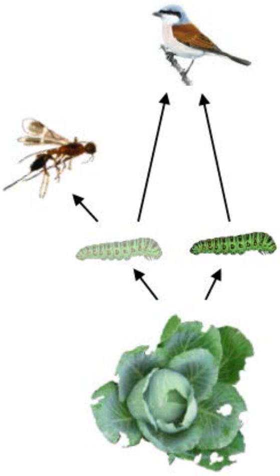

Figure 5.2. One scenario for vertebrate intraguild predation based on the model system of Martin et al. (2013). Parasitoids wasps reproduce by laying their eggs in herbivores (caterpillars). Developing parasitoid larvae kill the herbivorous host after a time lag. Birds feed on both parasitized and non-parasitized caterpillars, thus impacting populations of the shared prey/host and indirectly of the parasitoids (*coincidental* intraguild predation).

5.2. The Model

As described above, our model is inspired by a cabbage-caterpillar-parasitoid-bird trophic network (Figure 5.2), described and analyzed in detail by Martin et al. (2013). This system is stable because the TP population dynamics do not depend on the herbivores or the MP, i.e. the TP may feed on potentially many other prey species and, due to its high mobility, forage widely in the landscape. The MP population dynamics are more closely linked to the herbivore dynamics, but we assume that refuges or large scale spatial structure exist that allow global persistence and continuous recolonization of previously extinct local MP populations.

More specifically we do not model plant dynamics explicitly. We assume that there is a stable and continuous but limited supply of resources for the herbivores. In our stochastic discrete time model the herbivores exhibit stochastic logistic growth. The mean number of offspring is drawn from a Poisson distribution with mean λ which is calculated according to the logistic growth model of Hassell (1975):

$$\lambda = \lambda_0 * \frac{1}{1 + \mathrm{a} * \mathrm{N}} \text{ with } \mathrm{a} = \frac{(\lambda_0 - 1)}{K}$$

The mesopredator is annual as the herbivores and consumes prey according to a Holling Type II functional response with is most commonly found in nature (Holling, 1959). The number of parasitized/ consumed herbivores is calculated as follows:

$$\mathrm{n_{consumed}} = \mathrm{N(MP)} * P_{max} * \frac{\mathrm{N(H)}}{E_{MP} * \mathrm{N(H)}}$$

with P_{max} as the maximal amount of prey items consumed per MP (the saturation of the Holling Type II functional response) and E_{MP} as the half-saturation constant of this function, i.e. the prey population size (N(H)) when exactly half the maximal amount of prey (P_{max}) is consumed. The number of resulting MP offspring is drawn from a Poisson distribution with the individual number of consumed prey as mean, weighted with the assimilation coefficient (λ_{MP}) which represents how many parasitoid larvae can feed on one parasitized herbivore.

As the TP dynamics are completely independent of H and MP population sizes, we model the TP simply as a mortality rate for H and MP. We assume that the TP feeds on herbivore larvae and that TPs may over-proportionally consume parasitized compared to non-parasitized larvae, as parasitized larvae are more conspicuous and less mobile than non-parasitized ones (Grosman et al., 2008).

These dynamics are modeled in a spatially explicit, fragmented landscape consisting of 128x128 local patches (generated in R version 2.15 with package “ecomodtools”; Chipperfield et al., 2011). The landscape includes two habitat types: agricultural habitat, containing the plants that herbivore larva feed on, and seminatural habitat in which the adult butterflies forage on floral resources. We simplify this system in our model and do not include different life stages. Instead we only model herbivore larva in agricultural patches and treat seminatural habitat as unsuitable for these. As the amount of resources the adults collect determines their fertility (income breeding), and as we assume local foraging, we determine the growth rate of the herbivores (λ) as a function of the amount of neighbouring seminatural habitat. This function is linear and reaches a maximum at λ_0 (which determines the slope) and is additionally characterized by its intercept λ_{base}, which can be interpreted as the fertility of herbivores if no seminatural habitat is present in the foraging range. This basal fertility results from floral resources present in agricultural patches such as weeds.

Both H and MP may disperse globally with a fixed rate ($d_H = 0.05$ and $d_{MP} = 0.2$).

This system of stochastic equations is iterated numerically for 1000 time steps (generations) and herbivore and MP population sizes are recorded. The full set of model parameters is shown in Table 5.1.

Table 5.1. Model parameters, tested values and explanation. Default values are shown in bold font.

Parameter	Tested values	Explanation
K	50, 100, **200**	carrying capacity of herbivores
λ_0	2, **5**, 10	maximal herbivore fecundity
λ_{base}	0, **0.5**, 1	herbivore baseline fertility, i.e. without neighboring seminatural habitat
d_H	**0.05**	dispersal rate of herbivores (global dispersal)
P_{max}	2, 4, **6**	maximal amount of prey consumed by mesopredators (saturation of Holling type II functional response)
E_{MP}	1, **2**, 3	search efficiency of mesopredators (half-saturation constant of Holling type II functional response)
λ_{MP}	2, 4, **6**	mesopredator fecundity (assimilation coefficient; no. of mesopredator larvae per parasitized prey item)
d_{MP}	**0.2**	dispersal rate of mesopredator (global dispersal)
$\mu_{TP}(unparasitized)$	0, **0.1**, 0.2, 0.3	mortality inflicted by top predator to unparasitized herbivore larvae
$\mu_{TP}(parasitized)$	0, 0.1, 0.2, **0.3**	mortality inflicted by top predator to parasitized herbivore larvae
pH	0.1,...,0.9	percentage of seminatural habitat
Hurst	0, **0.5**, 1	Hurst coefficient of landscape, i.e. autocorrelation

5.3. Results

Our simple IGP model clearly shows that the outcome of such a trophic interaction depends on the composition – i.e. the relative amount – and on the spatial configuration – i.e. the degree of autocorrelation – of relevant habitat types (Figure 5.3). Depending on these two factors IGP may not always lead to higher densities of the common prey, here herbivores (H). This phenomenon of higher herbivore densities through IGP is commonly predicted (Polis and Holt, 1992; Holt and Polis, 1997) and occurs because top predators release predation pressure on the common prey by reducing the densities of mesopredators (MP or IGPrey).

We generally confirm this pattern for high fractions of seminatural habitat, i.e. abundant adult resources, and low spatial correlation of habitat types (Figure 5.3A,B). As habitat becomes more autocorrelated and adult resources rare (low fraction of seminatural habitat), this pattern is inverted and IGP reduces herbivore densities (Figure 5.3B,C).

This inversion of the effect of IGP crucially depends on the efficiency of the mesopredator and on the preference of the top predator for unparasitized v.s. parasitized herbivore larvae. With (i) more efficient mesopredators (higher search efficiency, higher maximal number of prey consumed, higher birth rates; Figure 5.4) and (ii) top predators showing a preference for parasitized larvae (results not shown), IGP is more likely to lead to less herbivory.

Our findings can be explained by taking a closer look at the population dynamics of mesopredators. It is well known that IGP may be unstable (e.g., Holt and Huxel, 2007) as a consequence of oscillations and one consumer being excluded. These dynamics are highly relevant to our results. As shown in Figure 5.5, a system consisting of only herbivores and mesopredators may be highly dynamic as a consequence of mesopredator extinctions and high turnover. This occurs as low fractions of seminatural habitat imply low adult resources and consequently low fertility and population densities of herbivores. In combination with an efficient mesopredator, such systems tend to be unstable and local mesopredator extinctions occur regularly. This turnover leads to more herbivory than in a comparable system with a constantly occurring mesopredator. The addition of a top predator to such a system stabilizes population dynamics (Figure 5.5). Although the top predator does reduce herbivore densities, this occurs at a constant rate and does not lead to more instability. IGP also reduces mesopredator population sizes and dampens oscillations, which stabilizes the system. As a consequence all three trophic levels coexist and herbivore population sizes are more efficiently reduced with IGP than without it.

5.4. Discussion

According to our model, the outcome of intraguild predation for shared prey depends on the spatial context of interactions, and is determined by both the relative amount of habitat types, and their degree of patchiness (autocorrelation). In some landscapes, for instance with low autocorrelation and a high proportion of seminatural habitat, IGP by a vertebrate top predator releases herbivores from mesopredator predation pressure, as predicted by theory (Polis and Holt, 1992; Holt and Polis, 1997). In other landscapes, notably with high autocorrelation or a low proportion of habitat, vertebrate top predators lead to additional herbivore reduction, despite IGP pressure on mesopredators.

These results confirm previous theory predicting a release of the shared prey by IGP (Holt and Polis, 1997) and expand it to spatially explicit systems. Release of the shared prey is predicted to occur in some, but not in all landscapes, and may be replaced in these landscapes by a reduction of the prey by top predators. This prediction is in

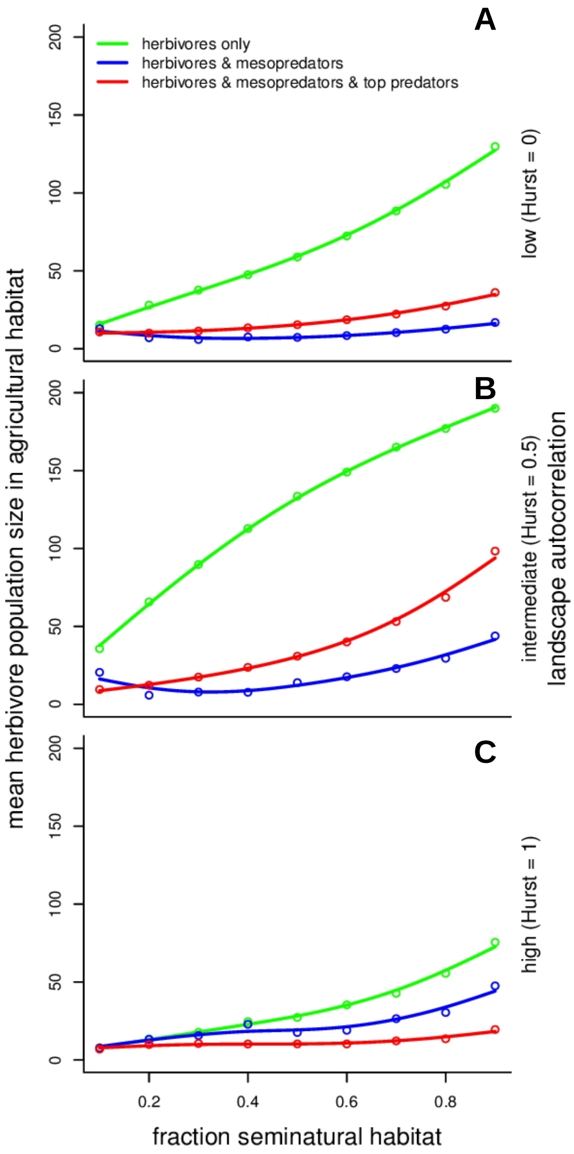

Figure 5.3. Mean herbivore population densities as a function of the fraction and the spatial configuration of seminatural habitat (mesopredator fertility: 4). Habitat autocorrelation increases from top to bottom. Green lines depict herbivore populations without any predation. Blue lines show the effect of adding one (meso-)predator (fertility: 4) and red lines include IGP. The circles represent means over 100 replicate simulation runs and the lines are smooth spline regressions (d.f. = 4). Parameters: K = 200, λ_0 = 5, λ_{base} = 0.5, d_H =0.05, P_{max} = 6, E_{MP} = 2, λ_{MP} = 4, d_{MP} = 0.2, μ_{TP}*(unparasitized)* = 0.1, μ_{TP}*(parasitized)* = 0.3.

agreement with previously unexplained empirical evidence, where vertebrate top predators appeared to reduce the shared prey instead of releasing it (Mooney et al., 2010)(Martin et al., 2013). The contrast observed in empirical studies between vertebrate and arthropod top predators, themselves generally associated with a release of the shared prey (Vance-Chalcraft et al., 2007), may be linked to differences in the spatial and temporal scales they experience. A landscape that is coarse-grained for arthropod predators and prey may appear fine-grained, with plenty of habitat resources, for vertebrates with high mobility and body size (Tscharntke et al., 2012). In addition, generation times of vertebrates are orders of magnitude longer than those of arthropods. The same landscape in a given time frame is thus associated with low population turnover of vertebrates (in our model equivalent to no variation), but strong

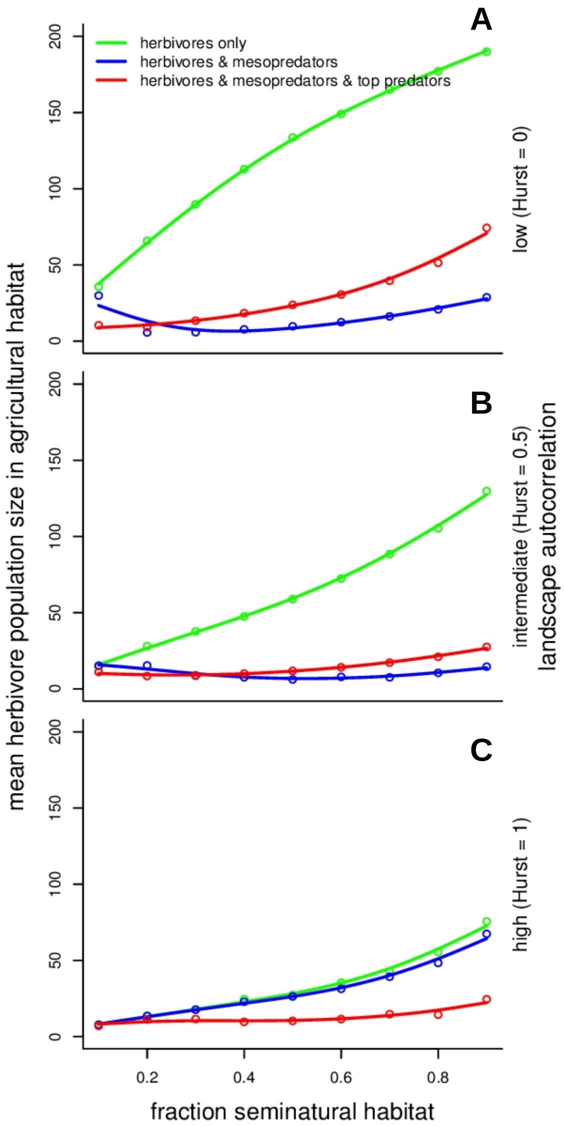

Figure 5.4. Mean herbivore population densities as a function of the fraction and the spatial configuration of seminatural habitat (mesopredator fertility: 6). Habitat autocorrelation increases from top to bottom. Green lines depict herbivore populations without any predation. Blue lines show the effect of adding one (meso-)predator (fertility: 6) and red lines include IGP. The circles represent means over 100 replicate simulation runs and the lines are smooth spline regressions (d.f. = 4). Parameters: $K = 200$, $\lambda_0 = 5$, $\lambda_{base} = 0.5$, $d_H = 0.05$, $P_{max} = 6$, $E_{MP} = 2$, $\lambda_{MP} = 6$, $d_{MP} = 0.2$, $\mu_{TP}(unparasitized) = 0.1$, $\mu_{TP}(parasitized) = 0.3$.

turnover of arthropod top predators, whose metapopulation response to the landscape context takes place at a comparable scale to arthropod mesopredators. Similar population variability of arthropod top and meso- predators may preclude the occurrence of a strong stabilizing effect of top predators on mesopredator-prey interactions, and as detailed below, lead to a release of the shared prey following classical intraguild predation theory (Holt and Polis, 1997).

When top predators are vertebrates, however, the outcome differs as a function of the landscape context. As shown in Figure 5.5 and Appendix 5.1, high local rates of extinctions of arthropod mesopredators take place in landscapes with little seminatural habitat, or with high autocorrelation, where interspersion between habitats providing either adult or larval resources for herbivores is low. These local extinctions are associated with low and/or heterogeneous herbivore populations in such landscapes, and reflect strong oscillations / instability of mesopredator-prey population dynamics. Adding a top predator to these systems stabilizes mesopredator dynamics, leading to less extinctions and higher overall pressure on herbivorous prey.

Elsewhere, e.g. in landscapes with low autocorrelation and high amounts of habitat, herbivore populations are a stable and abundant resource for mesopredators. Mesopredator dynamics thus show low variability, as reflected by low rates of local extinction. Instead of stabilizing these dynamics, addition of a top predator to such a system that is already stable only reduces mesopredator populations and thus predation pressure on the shared prey, causing its release.

The specificity of this model and its results lies with the dependency of shared prey on more than one habitat, each associated with a different life stage of the herbivores. Herbivore populations are determined by the amount of larval resources found in agricultural patches, but also by the fertility of adults, which depends on the floral resources found in seminatural habitats. It is at this level that space is important and determines the stability of herbivore populations. In the model, adult herbivores emerging in agricultural patches may disperse, and after successful dispersal are able to forage in their immediate surroundings (nearest neighboring patches) for floral resources. The relative amount and proximity of seminatural habitat, i.e. floral resources, then determines their fecundity, and in turn the dynamics of mesopredators.

Based on these results, we emit the following hypothesis. In general, IGP should lead to increased herbivore density due to release from mesopredator pressure, except if mesopredator populations tend to be locally unstable relative to top predators. Then, addition of top predators should act as a stabilizing factor for mesopredators, and herbivore density should further decrease. In empirical studies of IGP, measuring the turnover dynamics of meso- vs. top predators at large spatial scales may yield important clues to predicting the outcome of multispecies interactions in real landscapes. The implications for biological control of herbivores by multiple natural enemies are that stable populations of top predators should be favored when mesopredators are known to be comparatively unstable, in space or in time. However, top predators should not be favored if top and mesopredator stability are comparable at large spatial and temporal scales.

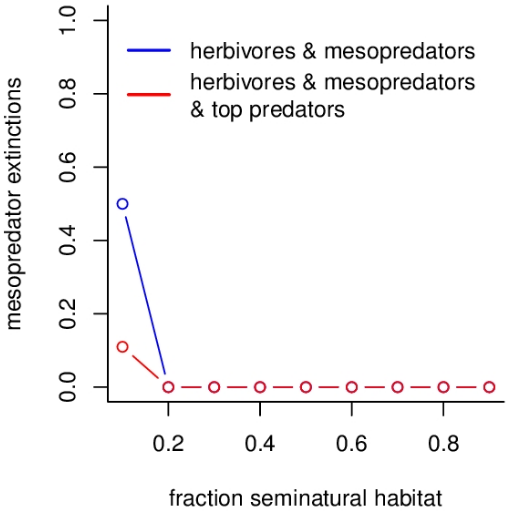

Figure 5.5. Extinction rate of mesopredators. Highly efficient mesopredators suffer frequent extinctions especially when herbivore fertility is low as a consequence of reduced adult feeding habitat. The addition of a top predator stabilizes this oscillating system and promotes the coexistence of all three trophic levels. Parameters: $K = 200$, $\lambda_0 = 5$, $\lambda_{base} = 0.5$, $d_H = 0.05$, $P_{max} = 6$, $E_{MP} = 2$, $\lambda_{MP} = 4$, $d_{MP} = 0.2$, $\mu_{TP}(unparasitized) = 0.1$, $\mu_{TP}(parasitized) = 0.3$, Hurst=0.5.

5.5. Acknowledgements

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5.7. Supplementary Figure

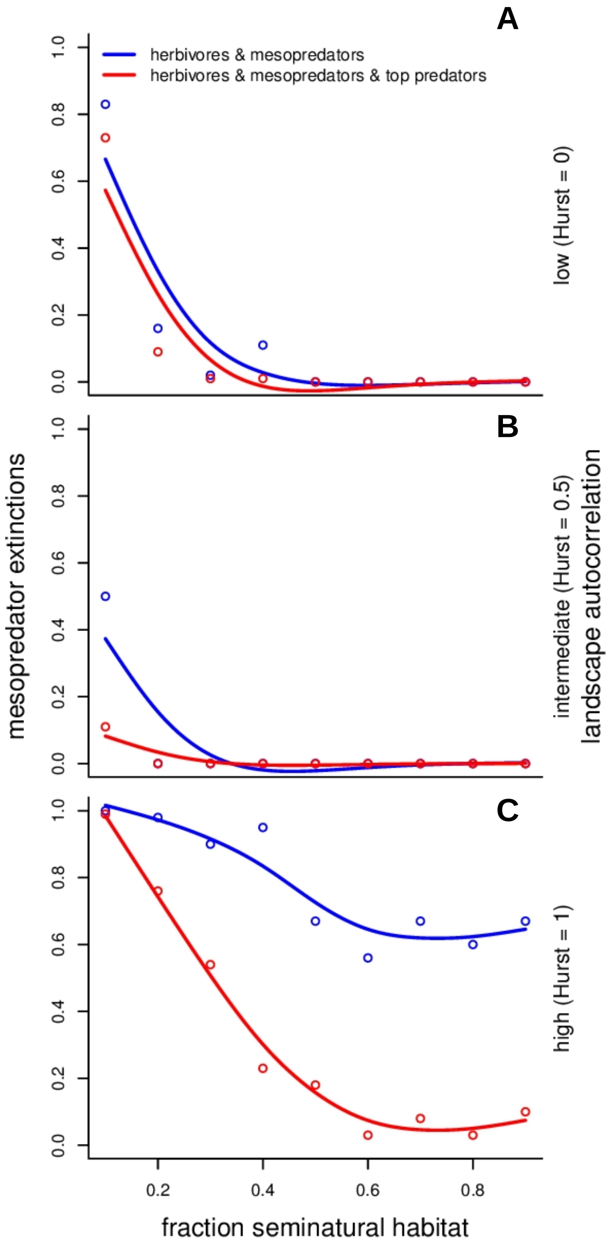

Figure S 5.1. Extinction rate of mesopredators at three levels of landscape autocorrelation. Parameters: K = 200, λ_0 = 5, λ_{base} = 0.5, d_H =0.05, P_{max} = 6, E_{MP} =2, λ_{MP} =4, d_{MP} = 0.2, μ_{TP}*(unparasitized)*=0.1, μ_{TP}*(parasitized)*=0.3, Hurst=0.5.

Complete list of publications

Peer-reviewed articles (published)

Martin, E.A., Reineking, B., Seo, B., Steffan-Dewenter, I., 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proceedings of the National Academy of Sciences of the USA 110, 5534–5539.

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Peer-reviewed articles (submitted and in preparation)

Fronhofer, E., Martin, E.A. Intraguild predation in a spatial context: the influence of landscape heterogeneity. *In preparation.*

Martin, E.A., Seo, B., Park, C.-R., Reineking, B., Steffan-Dewenter, I. Scale-dependent effects of landscape composition and configuration on natural enemy diversity and biological pest control. *In preparation.*

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Declaration / Erklärung

I hereby declare, to the best of my knowledge and belief, that this thesis does not contain any material previously published or written by another person, except where due reference has been made in the text. This thesis contains no material previously accepted or definitely rejected for award of any other doctoral degree at any university or equivalent institution.

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