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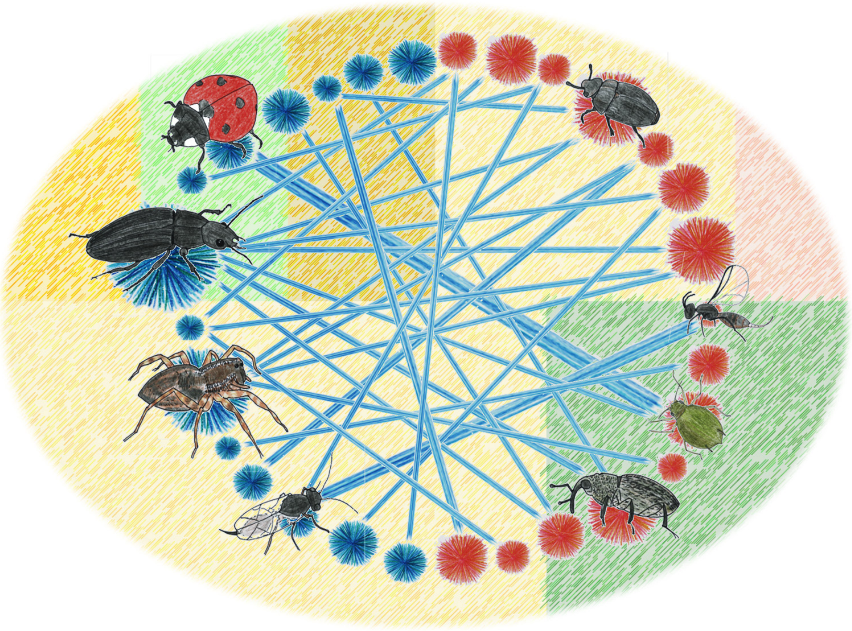
Local and landscape-level impacts of agricultural intensification on arthropod communities and their interaction networks

Guillermo Aguilera Núñez



Local and landscape-level impacts of agricultural intensification on arthropod communities and their interaction networks

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Abstract

Arthropods play a central role in agricultural landscapes being responsible for the delivery of many ecosystem services such as pollination, biological pest control, and nutrient cycling. But the current global decline of arthropods is intensified by habitat modification, loss and fragmentation, pesticide use and other intensive management practices. Thus, it is crucial to understand how such impacts affect ecosystem services provisioning.

In this thesis, I aim to explore how the management of local crop fields and landscape composition affect beneficial arthropod communities at different levels, including abundances and diversity of species and species interaction networks. I focus on predaceous and parasitic insects that provide biological pest control and pollinators. I assess i) how crop diversity affects arthropod diversity, ii) how fertilisation affects the local predator community and pest control, iii) how crop type (annual vs perennial) and landscape composition affect the predator-prey and host-parasitoid interaction networks and the implications for pest control.

I found that increasing crop diversity in landscapes with a high proportion of semi-natural habitats can enhance the diversity of beneficial arthropods. I also detected that organic fertilisation can benefit the abundance of local predators while specialist predators that move into the crop from the surrounding habitats boost biological pest control. I also found that crop type and landscape composition have effects beyond community species composition as also the interaction networks were altered, modifying the network stability and pest control potential.

My findings suggest that the main drivers of change in agricultural landscapes affect arthropod communities at different levels. Effects of habitat type and local management can be observed not only in the community composition, but some of the consequences were also reflected in the species interaction networks. Finally, I show that food web ecology can link community composition and ecosystem service provisioning.

Keywords: Crop diversity, Fertilisation, Community composition, Pest control, Pollination, Species interaction, Robustness, Apparent competition

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Effekter på lokal och landskapsnivå av intensifiering av jordbruket på leddjurssamhällen och deras interaktionsnätverk

Sammanfattning

Leddjurer spelar en central roll i jordbrukslandskap då de leverar många ekosystemtjänster som pollinering, biologisk skadedjursbekämpning och näringsomsättning. Men den nuvarande globala nedgången av leddjur förstärks av modifiering, förlust och fragmentering av livsmiljöer, användning av bekämpningsmedel och annan intensiv markanvändning. Därför är det avgörande att förstå hur sådana effekter påverkar ekosystemtjänsterna.

I denna avhandling ämnar jag undersöka hur lokal markanvändning och utformning av landskapet påverkar nyttiga leddjursamhällen på olika nivåer, inklusive från antal och mångfald av arter och nätverk av artinteraktioner. Jag fokuserar på rovleddjurer och parasitiska insekter som tillhandahåller biologisk skadedjursbekämpning och pollinering. Jag bedömer i) hur växtmångfald påverkar leddjurens mångfald, ii) hur gödsling av det lokala odlade fältet påverkar rovdjurssamhället skadedjursbekämpning, iii) hur livsmiljö och landskapsammansättning påverkar interaktionsnätverken för rovdjur-bytes och värd-parasitoid och konsekvenser för skadedjursbekämpning.

Jag fann att en ökad mångfald av odlade grödor i landskap med en hög andel naturliga livsmiljöer kan öka mångfalden av nyttiga leddjur. Jag upptäckte också att organisk gödning kan öka antalet lokala rovdjur medan specialiserade rovdjur som rör sig till grödan från de omgivande livsmiljöerna, ökar den biologiska skadedjursbekämpningen. Jag fann också att livsmiljötyper och landskapskomposition har effekter utöver samhällets artsammansättning där även interaktions-nätverken förändrades vilket påverkade nätverkens stabilitet och potentialen för skadedjursbekämpning.

Mina resultat tyder på att de viktigaste drivkrafterna för förändring i jordbrukslandskap påverkar leddjurssamhällen på olika nivåer. Effekter av naturtyp och lokal förvaltning kan observeras inte bara i samhällssammansättningen, utan några av konsekvenserna återspeglades också i artens interaktionsnätverk. Slutligen visar jag att fööväysekologi kan koppla samman gemenskapssammansättning och tillhandahållande av ekosystemtjänster.

Nyckelord: Växtdiversitet, Befruktning, Gemenskapens sammansättning, Skadedjursbekämpning, Pollinering, Artinteraktion, Robusthet, Tydlig konkurrens

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Dedication

To those of you who were always there when I needed you the most

To live in harmony with nature, we must know how to sing the same song as nature. To do that, we must understand nature. Good intentions aren't enough. Science might be – if we use it wisely.

Terry Pratchett, The Science of Discworld

Contents

List of publications

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

I. Guillermo Aguilera, Tomas Roslin, Kirsten Miller, Giovanni Tamburini, Klaus Birkhofer, Berta Caballero-Lopez, Sandra Ann-Marie Lindström, Erik Öckinger, Maj Rundlöf, Adrien Rusch, Henrik G. Smith and Riccardo Bommarco (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. Journal of Applied Ecology, (in press).

II. Guillermo Aguilera, Laura Riggi, Kirsten Miller, Tomas Roslin and Riccardo Bommarco. Organic soil fertilisation enhances local predator abundances and suppresses aphid growth. (manuscript)

III. Guillermo Aguilera, Giovanni Strona, Riccardo Bommarco, Benjamin Feit, Mattias Jonsson, Tomas Roslin and Kirsten Miller. Global change impacts on the robustness of predator-prey interaction networks in agricultural landscapes. (manuscript)

IV. Kirsten Miller, Guillermo Aguilera, Riccardo Bommarco and Tomas Roslin. Land-use intensity affects the potential for apparent competition within and between habitats. (manuscript)

The contribution of Guillermo Aguilera Núñez to the papers included in this thesis was as follows:

I. Main author. Conceived the project together with RB, assembled and analysed the data, and led the writing of the manuscript.

II. Main author. Conceived the project together with LR, TR, KM and RB, conducted the experiment, analysed the data and led the writing of the manuscript.

III. Main author. Conceived the project together with RB, TR and KM. Conducted the field experiment, analysed the data with GS, and led the writing of the manuscript.

IV. Second author. Conceived the project together with RB, TR and KM. Conducted the field experiment, and contributed to the writing of the manuscript.

Abbreviations

bp	base-pair
COI	mitochondrial cytochrome oxidase I gene
GIS	geographic information system
OSR	oilseed rape
OTU	operational taxonomic unit
pAC	potential for apparent competition

1. Introduction

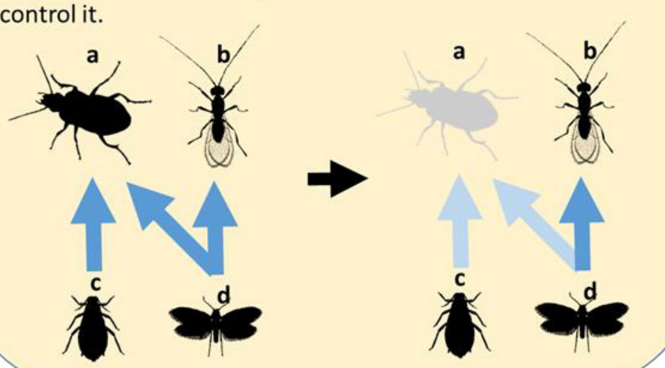
1.1 Communities and food webs

A community is a group of two or more species inhabiting the same place (Vellend, 2010). Community ecology is, thus, the examination of how species interact in space and time and an important aim of community ecology is to reach an understanding of how global changes, particularly human activities, impact communities.

Traditionally, when investigating the impact of human activities in nature, researchers focus on individual species, or groups of species, and tend to simplify complex communities by using simple metrics such as species abundance, richness and evenness to describe them. However, communities are more than an aggregation of species. Species have specific characteristics or traits that determine their roles and niches within the communities. These roles determine who interacts with whom, as well as the strength and the direction of the interaction. We can, therefore, describe the species in a community as nodes and connect these nodes with links that represent biotic interactions between them. Considering species interactions gives us a different perspective that allows us to answer specific questions regarding the dynamics and stability of the species populations that form the community (Box 1). But, these links between species are rarely one-to-one relationships, they are all part of greater and more complex interaction networks between different compartments of the community. Network or food web ecology can therefore provide a new framework to quantify both the diversity and the function of ecological communities (Thompson et al., 2012).

Box 1: Using networks

The figure below represents an oversimplified community composed of two prey species (“c” and “d”) and two natural enemies (“a” and “b”). The blue arrows represent existing interactions between a prey and its predator. If changes would negatively affect the population of the predator “a” and it would disappear from the community, we would lose the links of the carabid beetle with their preys, so the predation pressure will decrease for the prey “c” and “d”. In the hypothetical case of an outbreak of the prey “d”, this herbivore has a natural enemy in the system that can control its growth but in the case of an outbreak of the prey “c”, this herbivore has lost its predator so it would be harder to control it.



From a more practical point of view, food web ecology can help us to identify species with important roles within the community and, more specifically, it can help us to understand the ecological processes that occur as a result of those interactions. But, ecological interaction networks in nature are complicated and rapidly increase in complexity as species and their associated interactions are added. As a result, the consideration of a subset of species and links within a complete ecological network can be a useful starting point to explore specific questions or the impact of keystone species on a particular guild (Figure 1). Additionally, we can use ‘network metrics’ to describe the overall properties of a network and use these to compare multiple networks, perhaps from different locations, to find general patterns that can be used to see how the interactions of an entire community change according to environmental drivers (Thompson et al., 2012).

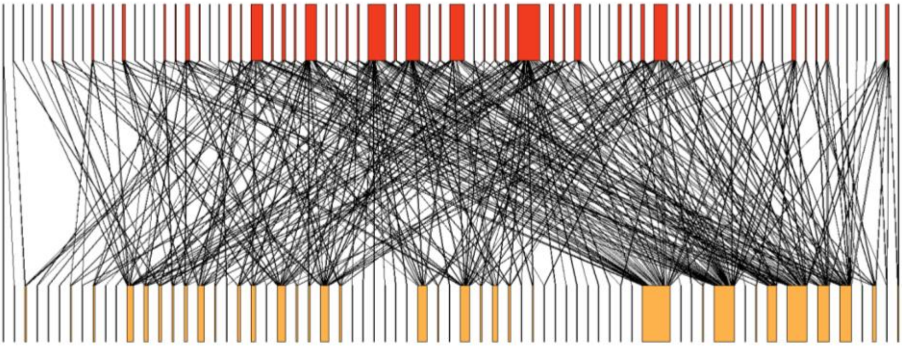


Figure 1. Predator-prey interaction bipartite meta-web for arthropods in Skåne (Southern Sweden). The upper level represents the predator species found across all sites for paper III, and the lower level shows the preys. The width of the bars represents abundances and the lines between both levels represent measure interactions. Image: Guillermo Aguilera.

For example, the ‘connectance’ of a network tells us the proportion of realised links between species out of the possible total; ‘generality’ informs us about the average number of prey items per predator; and the ‘robustness’ helps us understand the level of secondary extinctions that could occur in the community in response to a perturbation (Dunne et al., 2002; Heleno et al., 2012; Kaiser-Bunbury et al., 2010). Thus, considering ecological communities as networks of interacting species gives us a new perspective that can be valuably used to tackle how species assemble and the consequences of their interactions.

1.2 Ecosystem functions and services

Communities are not static, their structure and composition vary over time. Such dynamics are driven by species interactions and the resulting direct and indirect effects on other species within the community. For example, if we think about a carnivore consuming a herbivore, an increase in abundance in the herbivore will then favour an increase in the carnivore abundance. As well as these direct implications, interactions can also elicit effects on other species within the community indirectly. In the previous example, the presence of the carnivore may indirectly benefit a plant species by suppressing the abundance of the herbivore that feeds on it. Predation, herbivory, decomposition … all these functions become more relevant when we can link them with direct benefits to humans and society. We use the term ecosystem services when we refer to the benefits provided by ecosystems that positively impact human well-being (Harrington et al., 2010).

The stability of ecosystems and the provision of services to humans are therefore the result of complex interaction networks between species. As a result, when we investigate the provision of ecosystem services and how to maximize them, or when we evaluate their future stability under the influence of global changes, we are asking questions that go beyond what species comprise the communities. Consequently, network ecology and the study of species interactions become the link between communities, their functioning and the provision of services.

1.3 Arthropod communities and their functions

Arthropods are one of the most diverse and widespread animal groups on the planet. Their diversity of adaptations made them capable of inhibiting any habitat and that is one of the reasons they play key roles in many environmental processes and the functioning of the ecosystems (Schowalter, 2013). For example, arthropods comprise the diet of a wide range of other animals, being part of the base levels of almost every food pyramid (Nyffeler et al., 2018). Soil arthropods, enhance soil decomposition and promote nutrient cycling that benefits primary producers (Stork and Eggleton, 1992). Pollinators are crucial to the provision of a high proportion of the food in our plates and arthropod predators control pests that affect the crops we grow (Bianchi et al., 2006; Ollerton et al., 2011). But arthropods can also cause us problems, for example when alien species establish in new habitats or when ecosystem degradation or global changes turn arthropods into a problem as insect pests or vectors for diseases (Kenis et al., 2009; Weintraub and Beanland, 2006). Arthropods also exhibit characteristics that make them excellent study organisms. They are highly diverse; easy to handle and to capture; and many can be strongly linked to specific habitats becoming precise bio-indicators. These reasons, in addition to their short life-cycles, make them a useful animal group for studying the effects of environmental change on ecological communities.

Arthropods are especially important in agricultural landscapes, (Losey and Vaughan, 2006). They hold crucial roles in crops as pests, pest controllers, pollinators and soil nutrient-cycling agents. Unfortunately, the general negative trends currently reported for arthropod diversity and abundance also impact those providing these ecosystem services (Brooks et al., 2012; Potts et al., 2010; Wagner, 2020). Pollinator declines are a consequence of habitat fragmentation and degradation, the use of pesticides, or the spread of pathogens (Bartual et al., 2019; Rundlöf et al., 2015). Similarly, ground-dwelling predators and providers of biological control, such as carabid beetles, are also affected by changes in the landscape and intensive agricultural practices (Vanbergen et al., 2005). These practices, specifically the ones targeting the management of the agricultural soil also have important consequences for soil arthropods that are part of the decomposer community (Wang et al., 2016).

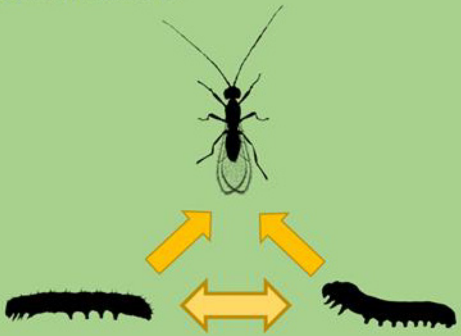
Figure 2. Seven-spotted ladybird beetle feeding on cherry-oat aphids on an oat plant. Photo: Guillermo Aguilera Núñez

The relationship between diversity or abundance of organisms and the level of ecosystem services provided by them is not always straightforward (Winfree et al., 2015). We need to consider species interactions to account for species roles. Here, functional diversity can be a better metric to quantify the diversity of a community if what we are after is the link between diversity and ecosystem services as predation or pollinator (Krauss et al., 2011; Woodcock et al., 2019). Functional diversity considers the “functions” and roles of organisms rather than their identity. This approach makes even more sense if we want to predict how the functioning or provision of services will respond to disturbances. E.g. if a community comprises multiple organisms with a similar set of traits and functions, the loss of a single species is unlikely to elicit a significant impact on ecosystem functioning as others will take its place. However, the loss of an organism with a unique set of traits in the community can trigger cascading effects (Borrvall et al., 2000). In fact, it is possible to measure the resilience of ecosystem services like biological control by considering the redundancy of predation within the predator community (Feit et al., 2019).

Furthermore, pest control and pollination are mediated by the interaction of two organisms, a predator consuming a prey or a pollinator visiting a plant. But such interactions do not occur in isolation from other species and interactions in the community. In fact, in some cases, pollination or pest control services can be driven by indirect effects resulting from interaction networks (Box 2). If we want to improve our predictions on pollination or pest control, we may want to consider the whole community of plants and pollinators or herbivorous pests and their predators, know who interacts with whom, and how strong these associations are. Thus, considering communities as networks of interacting species, we can reveal certain patterns that clarify how the changes can affect the whole community and its functioning.

Box 2: Apparent competition

The figure above represents a parasitoid that lay eggs in two herbivore species. The dark orange arrows indicates the direct host-parasitoid links. The light arrow linking the two herbivores represent the apartment competition between them. This indirect interaction is negative because when one of the herbivore species population grows, the parasitoid population grows following the increase of food resources. But ultimately, an increase of the parasitoid population will have detrimental effects on the second herbivore.



1.4 Global Changes

Global changes, especially climate warming and the degradation and transformation of habitats by humans are reshaping the world´s surface at a steep rate. Temperatures are expected to increase on average by 1.5 °C until the end of this century (IPCC, 2014) and almost 60% of the land has been already transformed to meet the demand of a growing human population (Ellis and Ramankutty, 2008). This abrupt modification of the habitats easily translates into negative consequences for the majority of species inhabiting them (Yalcin and Leroux, 2018). As a result, we are experiencing a rapid increase in the extinction rates of many taxa (Thomas et al., 2004; Urban, 2015). Arthropods are no exception, and the most recently reported trends show steep declines of arthropod populations (Seibold et al, 2019; Klink et al. 2020).

Climate change is expected to heavily affect the distribution and abundances of arthropod species in agricultural landscapes (Sharma & Dhillon, 2018). Additionally, for arthropods inhabiting the agricultural fields, local land management and the configuration of the surrounding landscape play an important role in determining their diversity (Seibold et al, 2019, Thorbek & Bilde, 2004).

Altogether, considering the current global trends of arthropod communities and knowing about their importance for ecosystem functioning, it becomes crucial to understand the implications of such global changes for species and their interactions. This is the only way we then can predict the status of arthropod communities in the future and how such situations can affect the functioning of the ecosystems but also take decisions that will mitigate the loss of services provided by them.

1.5 Local and landscape-level impacts on arthropod communities in agricultural landscapes and the services that they provide

Overall, the current trends in global changes indicate that the uncertain future of arthropod communities in the agricultural landscapes can result in the loss of many of the services they provide to our benefit. Thus, it seems crucial to answer several questions about the arthropod communities in agroecosystems: what are the drivers of species composition in agricultural landscapes? What determines the provision of ecosystem services by those communities of arthropods? Does the use of networks provide a better understanding of the provision of ecosystem services and their future stability?

1.5.1 Local land management

It is well established that local conditions shape arthropod communities. From the broader context, some species are most likely to be found only in certain habitats due to a process called ‘environmental filtering’, that assumes that environmental conditions will select for species that can persist in a certain habitat (Li et al., 2017). In the case of agricultural landscapes, we find arthropods that are specialised to specific crop types (Weibull et al., 2003). The most common cases are herbivores that are adapted to feed on particular crops, e.g. aphids on cereal crops. Thus, crop type filters from the species found in the landscape pool to the ones we can find in a field. However, many species inhabiting the agricultural landscapes are generalists. This means that they possess a set of traits that allows them to inhabit and forage in a wide range of habitats. Thus, for those generalist species, the management of crop fields is an even more important source of disturbance for local communities that can have rapid effects on the species composition and functioning of the ecosystem (Batáry et al., 2012; Birkhofer et al., 2008; Boutin et al., 2009).

When thinking about management practices that are detrimental to local arthropod communities, the use of pesticides is probably the first management that comes into mind (Ricci et al., 2019; Rundöf et al., 2015). But pesticides are not the only common practice that can have a marked effect on the local arthropod communities. Generalist predators like carabid beetles, for example, can complete their entire life cycle within the same field (Kromp, 1999), so local practices and the management intensity will be crucial to the development of certain species (Holland and Luff, 2000). Crop rotation regime can increase both the abundance (Bourassa et al. 2010; Patterson et al. 2019) and the community assemblage of carabid beetles (Ellsbury et al. 1998) and conventional tillage reduces ground-dwelling arthropods (Tamburini et al. 2016). We can therefore encourage the establishment of our desired arthropod community by carefully choosing the management practices we apply. For example, practices like the use of organic fertilisers, conservation tillage or allocating parts of the fields to flower strips or other refugia for arthropods have been proven to benefit arthropod communities (Birkhofer et al., 2008; Rundlöf et al., 2018; Schellhorn et al., 2008; Tamburini et al., 2016).

1.5.2 Landscape composition

Most of the natural enemies, pollinators and pests in agricultural landscapes are mobile organisms so landscape ecology is a keystone in the study of these arthropod communities (Chaplin-Kramer et al., 2011; Diekötter et al., 2008; Samways, 1989; Zaller et al., 2008). As a result, we have a large literature body on how landscape characteristics can define arthropod communities. The current negative trends in arthropod abundances and species richness are associated with changes in land use that induce habitat loss and reduce landscape connectivity (Uchida and Ushimaru, 2014).

The conversion of natural habitats into farmland and the rapid elimination of hedgerows and other habitats that can act as refugia or overwintering sites for arthropods creates new habitats where the dispersion and spillover from natural habitats become harder (Blitzer et al., 2012; Rand et al., 2006).

Contrarily, the proximity of semi-natural habitats at the landscape level can enhance the presence of beneficial arthropods (Holland et al., 2017). Increasing the temporal and spatial heterogeneity of the agricultural landscape can enhance the abundances of mobile species (Bertrand et al., 2016). Therefore, moving from monocultures to landscapes where more crop species are grown and diversifying management practices should result in heterogeneous agricultural landscapes that provide arthropods with a wide range of resources to use at different times of their developmental stages (Bertrand et al., 2016; Hass et al., 2018). Enhancing floral resources for pollinators or habitats that provide shelter or alternative prey for natural enemies can increase the richness and abundances of these beneficial arthropods (Woodcock et al., 2014, Snyder, 2019).

1.5.3 Local and landscape effects on networks and ecosystem services

Interest in studying ecological networks has increased over the last decade. The use of metrics and characteristics of interaction networks has the advantage of being able to describe the stability of communities (Mougi and Kondoh, 2016) and their use can become more important if we can translate them into the stability of ecosystem services. There is much scientific evidence to indicate that ecosystem services are affected by environmental change in a similar way to the organisms that are responsible for their provision. As an example, agricultural intensification via landscape simplification can reduce the level of pest control provided by natural enemies (Rusch et al., 2016) and visitation rates of pollinators decrease with increasing isolation from natural habitats (Ricketts et al., 2008). But, can we draw such direct conclusions based on species responses? Can we use network interaction metrics to disentangle the relationship between community composition derived from traditional metrics (abundance, richness and diversity), species interactions and the delivery of ecosystem services?

During the last decade, we have compiled a considerable amount of knowledge about how network metrics change in space and time, and what are the causes and consequences of such changes. For example, habitat modification can alter host-parasitoid networks by altering the evenness of the interactions, the specialisation level of some parasitoids and the parasitism rates (Tylianakis et al., 2007). These changes in the interaction network, however, were not detected by conventional community descriptors. Similarly, local management like the use of fertilisers can increase the connectance and attack rates in host-parasitoid networks (Fonseca et al., 2005; Macfadyen et al., 2009).

Landscape composition can also alter species interaction networks. The complexity of the surrounding landscape can reduce the complexity of host-parasitoid networks by increasing the dominance of one of the herbivores (Gagic et al. 2011) and inter-annual land cover changes of agricultural landscapes can affect unsymmetrically the different levels of a plant-herbivore-parasitoid interaction network (Thies et al., 2008). Complementarity in a network can explain how two parasitoids can coexist using different strategies or traits that allow them to attack different prey species, but also can explain parasitism rates in time and space (Peralta et al., 2014; Sanders et al., 2018).

It is becoming more and more common to find examples of the use of network ecology to approach functions like parasitism or pollination that are valuable ecosystem services (Bartomeus et al., 2008; Kaiser-Bunbury et al., 2010; Peralta et al., 2014; Tiedeken and Stout, 2015; Tylianakis et al., 2006). Predator-prey interactions, however, are harder to characterise and they have not been studied as extensively as other interaction types (Roubinet et al., 2018). Observing predator-prey interaction among arthropods is not always possible and we need a new methodology to collect such data. Within the last decade, new sampling techniques involving the meta-barcoding of gut contents have become available and more accessible. Thus, by taking advantage of such techniques we can describe complex predator-prey interaction networks (Roslin and Majaneva, 2016).

2. Aims

In my thesis, I examine how landscape configuration and local management or environmental characteristics affect the structure of local communities. I investigate these effects on the diversity of local communities, the resilience of species interactions and the ecosystem functioning. This is done in the following four projects:

In **paper I**, I assess the effect of landscape crop diversity on the diversity and abundance of local beneficial arthropods: ground-dwelling predators and wild pollinators. Specifically, I test for the interactive effect of crop diversity and the semi-natural habitat proportion in the landscape.

In **paper II**, I investigate the effect of local and landscape subsidies in agricultural landscapes in the form of fertilisation and incoming predator species from the surrounding landscape and their effect on the top-down and bottom-up control of a herbivore pest. I further consider the interaction of both factors and the outcome in terms of pest control and yield production.

In **paper III**, I assess the influence of landscape configuration and local habitat characteristics on local arthropod communities and predator-prey interaction networks. Further, I assess the robustness of pest control under different global change scenarios.

In **paper IV**, I examine the influence of landscape configuration and local habitat characteristics on local host-parasitoid communities. Specifically, I explore the impact of these drivers upon indirect effects by investigating the potential for apparent competition between herbivorous arthropods.

3. Methods

3.1 Study systems

In my thesis, I carried out two field experiments in three types of crops: oilseed rape, ley and oat. These crops are representative of the commonly grown crops in the Swedish agricultural landscape. Each of them has distinct characteristics that make them particularly appropriate for addressing our questions about how local and landscape-level disturbances affect different aspects of arthropod communities.

Figure 3. Field of winter OSR in full bloom in Skåne. Photo: Guillermo Aguilera Núñez

Winter oilseed rape (*Brassica napus L.,* OSR) fields are annual crops and are extremely common in the landscapes of the southernmost part of Sweden.

They enhance the flowering resources in the landscape for pollinator species when the crop is in flower for about two-three weeks (between April and May). Importantly, OSR yields are significantly increased by insect pollination (Bommarco et al., 2012). OSR crops require intensive management including the preparation of the soil or the use of external inputs like pesticides and fertilisers. The crop is also attacked by several well-studied herbivorous arthropod pests which cause economically significant losses to farmers. The complex herbivore pest communities, composed of pollen beetles, pod midges and weevils among others made this system perfect to examine differences in the assemblage of host-parasitoids and predator-prey interaction networks.

Ley fields are a mixture of grass and legumes usually harvested for silage, covering extensive areas of the Swedish agricultural landscape. They are commonly grown as part of long crop rotations (Rusch et al., 2013), staying in the same field for two to four years. This makes ley fields really unique where the management is minimum and the disturbances almost insignificant. Including a treatment with such low management inputs allows the comparison of arthropod communities and predator-prey interactions with the more intensively managed field, OSR (Hanson et al., 2016).

Figure 4. Common edge between a ley field, characterised by a low management intensity, and an OSR field in Skåne. Photo: Guillermo Aguilera Núñez

Finally, oat fields were also considered. I selected this type of crop because cereal fields are predominantly attacked by a single herbivorous pest species, the bird cherry-oat aphid (*Rhopalosiphum padi L.*). Focusing on a single pest species allowed me to explore predation effects upon their growth and how different predator communities or management regimes will affect the plant quality and final yield.

Figure 5. An oat plant attacked by aphids. Photo: Guillermo Aguilera Núñez

3.2 Landscape crop diversity effects on arthropod communities (Paper I)

To investigate landscape effects such as the crop diversity and the proportion of semi-natural habitats on the local arthropod communities, I took advantage of datasets that were generated as part of previous studies carried out within the agricultural landscapes of the south of Sweden over the last decade, including my own (**paper III and IV**). Focussing on studies targeting predaceous arthropods or pollinators in two main crop types in the region: OSR field and cereal fields, we obtained information about carabid, spider and pollinator communities for 7 studies, for a total of 154 individual field sites.

The sampling methodology for these types of arthropods has been well established and standardised in this field (Bater, 1996). In our case, all the studies used the same sampling methodology: pitfall traps for ground-dwelling predators and transect counts for pollinators. These similarities allowed us to merge the information from different studies and we could account for the difference in sampling effort by using the number of pitfall traps used and the number of days they were collecting as well as the duration of pollinator transects and the total area they covered. We only selected data from sampling points within the crop field and controlled for distance from the edge before calculating the total carabid, spider and pollinator abundances and diversity (Shannon index) for each field.

For characterising the agricultural landscape we used a farmland GIS layer from the Swedish Agricultural Board, which contains information about the type of crop grown at any farm in a specific year. After obtaining the identity and the cover of all crops growing within a 1km radius from the field sites we calculated a Shannon index that would reflect the diversity of crops in the landscape. Additionally, we used a digitalised Swedish topographic map (Terrängkartan, Lantmäteriet, 2018) to add information about other land uses as semi-natural grasslands, forests, urban and water cover. With this layer, we calculated the cover of semi-natural areas in the landscape (semi-natural grasslands + forest) and we confirmed that the amount of urban and water cover was negligible. All landscape analyses were done in ArcMap software, version 10.3.1 (ESRI, USA).

3.3 The effects of local and landscape subsidies on arthropod communities (Paper II)

In **paper II**, I examine how important local and landscape subsidies are for the provision of ecosystem services via changes in the arthropod communities. On one hand, the addition of fertiliser to increase crop yield is a common practice that can have implications for the local arthropod community. On the other hand, pest suppression relies on predators that immigrate from the surrounding landscape into the focal crop. These local and landscape subsidies can affect different guilds within the arthropod community (soil mesofauna and soil predators) and the interactions between predators, herbivores and the crop, e.g. pest control on the growth of a herbivore population, the amount control provided by the predators, the amount of control provided by the plant via bottom-up processes, and the final yield.

To understand the interaction between these local and landscape level processes, I designed an experiment where I could manipulate both the use of fertilisers and the species of predators moving between the surrounding landscape and the crop. I carried out this study in an experimental field where fertilisation treatments have been applied since 1996. We used three fertilisation treatments: manure fertilisation, inorganic fertilisation and unfertilised plots. Each fertilisation treatment was replicated in four independent blocks.

To simulate the addition of predators moving from the landscape into the crop field we manipulated the predator community. With this aim, we took a mesocosm approach. A mesocosm is an outdoor experiment under controlled conditions. For this purpose, we used cages (2x2x2 meters) consisting of metal frames covered by a fine mesh and dug 20 cm deep in the soil to prevent the entrance of external arthropods at the ground level. We placed three cages in each plot so we could manipulate the natural enemy communities in three ways: no additional predators, additional spiders (generalists) and additional spiders and ladybird beetles (generalists and specialists respectively). In total, we used 36 cages (three fertilisation treatment x three predator treatment x four replication blocks).

To measure the effect on soil mesofauna, I extracted 2 cores of soil (down to 15-18 cm depth) at three times during the sampling session. One early in the season, another during the predation experiment and the last one just after removing the cages. I extracted soil mesofauna from each core using Tullgren funnels.

To measure the emergence of soil predators I emptied the cage of predators manually and using pitfall traps just after the cages were set-up. Then, I opened new pitfall traps to collect adult carabid beetles emerging from the soil.

Additionally, to capture the density of carabid beetles during the experiment I opened pitfall traps three times during the predation experiment.

To measure the effect of pest control on the growth of a herbivore population I inoculated some plants inside of the cages with aphids (*Rhopalosiphum padi L.*) and measured their growth.

Figure 6. Mesocosm experiment for predator community manipulation in an oat field. Photo: Guillermo Aguilera Núñez

The yield of each cage was hand-harvested just before removing the cages from the plots and weighted separated for seeds and straw.

To disentangle the top-down and bottom-up effects taking part in the biocontrol of the herbivore pest and the plant biomass creation, I installed additional exclosures within each cage. If we consider the cages as mesocosms where aphids are free to grow and predators are free to move (+A+P); then I added an exclosure where aphids were able to grow in absence of predators (+A-P) and another exclosure where oat plants grew in absence of aphids neither predators (-A-P). I measured aphid growth and yield inside the exclosures so this allowed me to i) calculate top-down (predation-mediated) effects on the aphid growth and plant biomass by comparing the density of aphids or plant biomass in +A+P and +A-P; ii) calculate bottom-up (plant-mediated) effects on the density of aphids by comparing +A-P exclosures in the different fertilisation treatments and 3) calculate bottom-up effects on the plant biomass by comparing -A-P exclosures in the different fertilisation treatments (for more detailed information on the top-down and bottom-up calculation see **paper II**).

3.4 Landscape-level and local effects on predator-prey and host-parasitoid interactions (Paper III and IV)

To address the wider question of how local and landscape-level impacts affect species interaction, in **paper III** and **paper IV**, I inspected how habitat type and landscape intensity shape local arthropod communities and their interactions. For this reason, I designed a field experiment consisting of 11 landscapes. Each landscape was composed of a set of two crop fields at its centre: a ley field adjacent to an OSR field. As described above, the differences between these two crops in terms of local management intensity make them ideal to study differences between them. Additionally, I measured the proportion of ley, OSR and other intensive crops as cereals covering the 1-km landscapes around the ley-OSR sites. I did this to account for the landscape intensity. All landscape analysis was done using the same methodology as in **paper I**.

To identify the ground-dwelling predator communities at each crop and site I used wet pitfall traps, opened for less than one week at four sampling events: before OSR flowering, during flowering (x2) and after flowering. Specimens were collected into 70% ethanol and morphologically identified at the lab. This data provides information on the diversity and abundance of predators at each site.

To characterise interaction networks between predators and their prey, and parasitoids and their hosts in OSR and ley fields I collected specimens within the fields and used DNA meta-barcoding to link predators to their prey items and hosts to their parasitoids.

3.4.1 Specimen collection for DNA metabarcoding: Predators

I sampled ground-dwelling predators using dry pitfall traps opened for 24 hours in two separate sessions (between the second and third wet pitfall trap sampling event) in both the ley and OSR habitats. The pitfall traps consisted of plastic cups (15 cm diameter) half-filled with clay balls. The addition of clay balls to the traps ensures a predator size-stratification to avoid intra-guild predation. Each trapped specimen was placed into an individual

Eppendorf tube containing 95% ethanol before storing at -20C until DNA extraction (within 3 months).

3.4.2 Specimen collection for DNA metabarcoding: Herbivorous hosts

Hosts were sampled in ley where an area 50m x 16m was sweep net sampled for 15 minutes in two separate days. I transferred the catches to plastic bags and stored them at 4°C until I could individually examine them for host specimens (within 12 hours of capture). Each host specimen was placed into an individual Eppendorf tube containing 95% ethanol before storing at -20°C until DNA extraction (within 3 months). In the OSR habitats, the host community was sampled differently due to the difficulty of using sweep nets in such a vegetation structure (OSR fields are dense and the plants can get quite tall). I, therefore, selected five OSR plants in the main transect (16 meters away from the crop edge) and beat-sampled them. This sampling was also done at two separate sessions. Following the same procedure as in the ley habitats, I stored the catches at 4C until I could individually transfer them into Eppendorf tubes containing 95% ethanol (within 12 hours of capture) and before storing at -20C. However, most of the OSR pests are specialists and their larvae develop inside the pods or deep in the flowers. To compensate for the low number of specimens obtained using the beating sampling I used a second approach. I collected the apical branch of a further ten OSR plants per site and was visually examined for any hosts. Specimens taken from these plants were then stored in the same way as other specimens.

3.4.3 Molecular characterisation of predator-prey and host-parasitoid networks

I used a DNA-metabarcoding approach to characterise interactions between both predaceous arthropods and parasitoids and their herbivorous preys and hosts. The details of the approach are given in **paper IV**, but in short, I adopted the following workflow:

We extracted DNA from the gut content of 4236 generalist predators and the whole body of 1693 larval specimens. For each extraction, a 316 base-pair fragment within the standard COI barcoding region of the mitochondrial Cytochrome c Oxidase subunit I gene was amplified. Taxonomic assignations were made against a COI reference database (derived from the

NCBI nucleotide database). Following Illumina sequencing and bioinformatic processing, we obtained a set of operational taxonomic units (OTUs), i.e. clusters of DNA sequences grouped based upon the DNA sequence similarity. Each OTU was then assigned a taxonomic ID based upon its similarity to DNA sequences within the reference database.

Before building the interaction matrices, we first removed all non-metazoan OTUs. Interaction matrices were then constructed by mapping all reads back against OTU sequences. Interactions that were only supported by a single read and samples with fewer than 100 metazoan reads in total were removed.

From the remaining samples, the identity of the OTU with the greatest proportion of reads for each specimen was recorded as the predator identity in the case of predator-prey interactions or the host identity in host-parasitoid networks. The identities were cross-referenced against the morphological identification of each specimen.

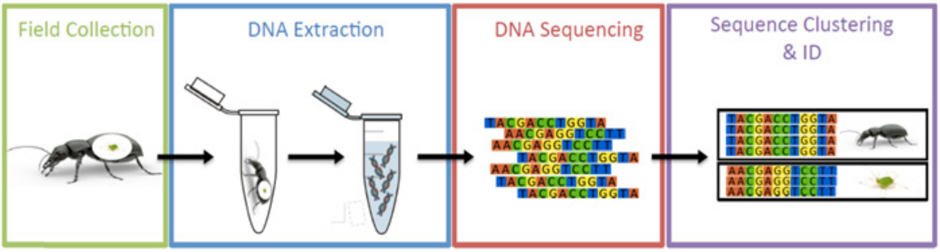


Figure 7. Molecular identification workflow of predator-prey interactions. Predators were collected in the field and individually stored in vials with ethanol. We extracted DNA from the guts of each predator (for small and medium predators we used the whole body). A 316bp fragment of the COI barcode region was then amplified and sequenced to provide us with multiple DNA sequences. Sequences were then clustered by similarity into OTUs. OTUs were IDed by comparing them to a sequence reference database. Image: Kirsten Miller.

The next step was to identify all other OTUs associated with each specimen. Predator gut content samples were screened for prey while herbivorous larvae samples were screened for parasitoids and these formed the basis of the interaction data.

In this way, predator-prey and host-parasitoid matrices were generated showing the frequency of association between each host and predator in each habitat and each parasitoid or prey. The resulting matrices were used to generate interaction networks and to calculate metrics such as the robustness of the network or the potential for apparent competition between herbivores.

3.5 Calculating the robustness of predator-prey interaction networks and their implications for pest control (Paper III)

To calculate the robustness of predator-prey interaction networks against global changes, I calculated three network metrics, which inform us about the stability of the associated pest control service. I used the predator-prey interaction networks generated from the DNA gut-content analysis in the ley and OSR fields from the 11 landscapes. I got a total of 22 habitat-site specific networks. However, I only used 20 networks since the other 2 were too small to be used in the predictions (less than five predators).

Following a commonly used approach for calculating robustness (Pocock et al., 2012), I used an algorithm to removed predators from each network and calculated the response in terms of a) the fraction of prey that remained with at least one predator controlling them in the network, b) the interaction strength at each removal and c) the changes in the modularity of the network. The two first metrics have clear implications in the robustness of the pest control since it quantifies the percentage of predators that are left without natural enemies in the system and how much “predation pressure” is lost at each step. While the third one explains clustering patterns in the network such that a high value indicates that the network can be subdivided into smaller groups of predators and herbivores interacting with each other but not with other groups in the community.

I assumed that species' reaction to global changes of different natures, and such changes will be driven by species traits. Therefore I run three simulations to explore how the robustness of predator-prey is affected by different global change scenarios:

a) Abundance scenario: in this simulation, I consider that rare species have a higher probability to go extinct compared to dominant species. Thus, I used the wet pitfall trap catches to give an abundance value to each predator species at each landscape and field. Then, the algorithm removed predators from the network from less to more abundant species.

b) Temperature scenario: in this simulation, I assume that species that are active at lower temperatures will suffer the negative consequences of climate warming before those adapted to higher temperatures. Thus, I used species temperature niches, based on pitfall trap catches that record the temperature at which species were collected. Then, the algorithm removed predators from the network from low to high-temperature tolerance.

c) Landscape intensification scenario: in this scenario, I assumed that some species are better adapted to landscape intensification than others. Thus, I calculated the response of each predator species to landscape intensification as the slope of a linear regression of each predator abundance as the function of landscape intensity, measured as the proportion of intensive crops in a 1km landscape. Then, the algorithm removed predators from the network from more to less affected.

d) Additionally, I ran three more scenarios: a random scenario to calculate the robustness of the networks facing random extinctions (null-model); a best-case scenario that removed species in such order that the robustness would be maximised at each case; and a worst-case scenario that removed species in a way that the robustness was minimised.

I run every model simulation 1.000 times to randomise ties and to obtain an average curve representing the proportional loss of each network metric at each predator removal step. To quantify the actual robustness I calculated the area under the curve (Pocock et al. 2012). Therefore, a community where all herbivores will remain controlled by predators until the last predator removal will have the maximum "robustness" of 1.

3.6 Calculating the apparent competition of host-parasitoid interaction networks and their implications for pest control (Paper IV)

To address the wider question of how local and landscape-level impacts shape indirect interactions in arthropod communities, in **paper IV** we used the host-parasitoid food webs to calculate the potential for apparent competition (pAC) between pairs of herbivores. The mechanisms of apparent competition consider that two hosts are connected by sharing a common parasitoid. An increase in the abundance of the first herbivore can enhance the parasitoid population that can increment its attack rates in the second herbivore (Holt, 1977). We adapted the apparent competition index from

Frost et al. (2016), which is an adaptation from the Müller index (Müller et al., 1999) to quantify the pAC between each host pair in the host-parasitoid network using the differences in abundances between the two hosts, the number of shared parasitoids between them, and the frequency of attacks.

Additionally, we modified this index to include the habitat where the hosts were sampled (OSR and ley fields), so I could calculate the effect of each host species upon other hosts within the same habitat and in the adjacent habitat. This distinction also allows us to measure the strength of apparent competition between ley and OSR communities. For a more detailed explanation of the equation see **Paper IV**.

The final aim was to find out if the information on apparent competition extracted from a host-parasitoid network could be used to predict the level of parasitism measured in the field. We, therefore, calculated expected attack rates using the abundances and pAC given by the metaweb (total regional web composed of the webs of all sites and habitats). We used two approaches to calculate expected attack rates based on equation 3 from Frost et al. (2016). In the first approach, we inferred attack rates using the abundance of the host and observed attack rates in the metaweb (excluding the site where the hosts were sampled to avoid circularity). For the second approach, we included the pAC for each host pair as well as the abundance of the second host. The idea behind these two calculations was that if expected attack rates show stronger correlation using the second approach, then it indicates that pAC influences realised attack rates of parasitoids upon herbivores.

4. Results and discussion

In this thesis, I present evidence of local management and landscape intensification affecting arthropod communities at different levels. In **paper I**, I found crop diversity and semi-natural habitats in the landscape to enhance the diversity of pollinators and predaceous carabid beetles. Predators moving from outside the crop can be crucial for pest suppression (**paper II**). But landscape intensity also influences the host-parasitoids networks with implications for pest control, as seen in **paper IV**. Local habitat configuration and management influence local communities as I show in **paper II** and **paper III** and can subsequently affect the structure of predator-prey interaction networks with important implications in its temporal stability.

4.1 Crop diversity effect on local arthropod communities

The configuration of the surrounding landscape will determine the local species pool found in crop fields. In this context, in **paper I**, I found that crop diversity enhances arthropod diversity in landscapes with a high proportion of semi-natural habitats. The interactive effect was greater when specifically inspecting the response of carabids and pollinators. The positive effect of patches of semi-natural habitats in agricultural landscapes such as forests, pastures and managed grasslands has been considered a piece of evidence for a long time (Bartual et al., 2019; Holland et al., 2017; Tscharntke et al., 2005). These results add an extra layer of knowledge: landscapes with semi-natural habitats can harbour a higher diversity of natural enemies by increasing crop diversity.

Carabid beetles are omnivorous ground-dwelling arthropods that are well adapted to agricultural landscapes and can benefit from a more heterogeneous crop composition in the landscape. The great diversity of carabid beetles is a result of the diversity of resources they are able to utilise (Spake et al., 2016). A varied crop composition means a wider range of resources for carabid beetles in terms of prey and refugia that would result in a more diverse carabid community. The same mechanism would explain the result for pollinators since a higher crop diversity would not only increase the temporal availability of resources such as prey but also of flowers and undisturbed crops such as ley fields. Spider diversity, however, remained unaltered with changing crop diversity or semi-natural habitats in the landscape.

My results also indicate that crop diversity does not increase arthropod diversity by default. Only landscapes with high semi-natural habitat cover are benefited. This may be explained by the fact that some of these predators and pollinators overwinter in semi-natural habitats.

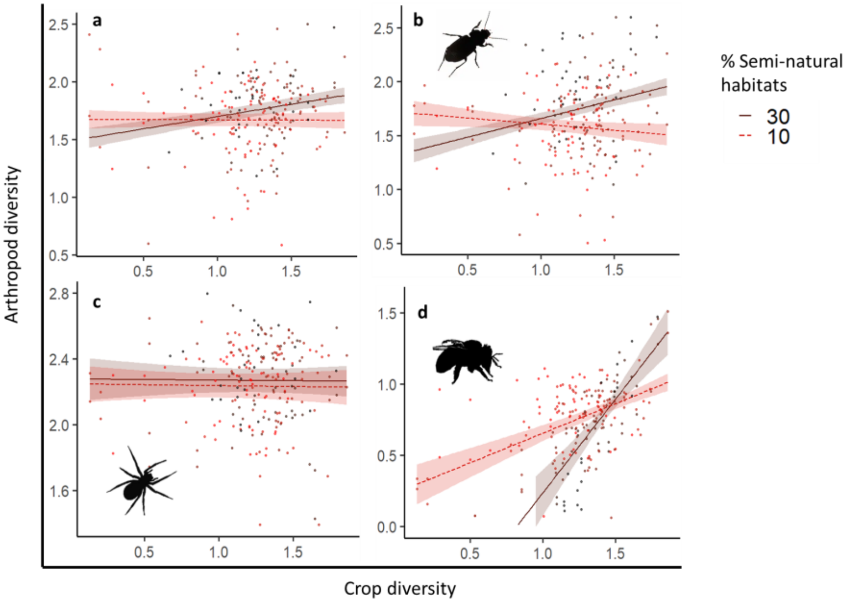


Figure 8. Effect of crop diversity on a) total arthropod diversity, b) carabid beetles, c) spiders and d) wild pollinators, in landscapes with high (30%, black line) and low (10% red line) proportion of semi-natural habitats. Model fitted lines and 95% CI. This figure is adapted from paper I.

Contrarily to the diversity, the abundance of arthropods was not affected by crop diversity. Semi-natural habitats, however, had negative effects on the total abundance of carabids but enhanced the abundance of pollinators. These results highlight the importance of semi-natural habitats for enhancing the number of pollinators with the provision of flower resources and nesting sites. Carabid beetle abundances, however, may be more affected by local management practices in the agricultural fields than the proportion of semi-natural habitats in the landscape.

4.2 Fertilisation and additional predators

4.2.1 Fertilisation effects

Local subsidies like the use of chemical and organic fertilisers are common practices that can determine the composition of local arthropod communities. In this context, in **paper II**, I found that manure-fertilised plots had the highest number of adult carabid beetles emerging from the soil compared to plots that received inorganic fertiliser or no fertiliser at all. I hypothesise this effect before the start of the experiment. I based this reasoning on manure fertilised plots harbouring a more abundant soil fauna that will sustain a more abundant ground-dwelling predator community. However, soil sampling did not show these effects. Soil fauna (other than carabids) was quite low and similar in every fertilisation treatment. The reason behind these low numbers of individuals may be the drought experienced at the beginning of the experiment that may have forced these organisms to move deeper in the soil profile. So, how to explain the differences in adult carabid emergence? I think that such differences can be due to better soil conditions in organic fertilised plots that will benefit and enhance the survival of larvae or adult carabids while overwintering (Noordhuis et al., 2001; Pfiffner and Luka, 2000).

I found that the use of fertiliser can greatly affect the herbivore community feeding on the crop plants. The growth of the aphid population feeding on the oat plants was significantly smaller in plots that received organic fertilisation while plants growing under inorganic fertilisation scored the higher densities of aphids. These results indicate that the rapid growth of biomass in plants that received inorganic fertilisation can increase the resources for the aphid population and trigger its growth. Manure fertilisation increases plant biomass but at the same time benefits the community of ground-dwelling predators.

But fertilisers are commonly used for benefiting not the arthropod community but the crop by increasing plant yield. Accordingly, I found that the use of fertiliser indeed increased the yield of the crop. Plants under the inorganic fertiliser treatment had the highest biomass and differences with both the control and the manure fertilised plots were significant. However, after partitioning the yield data into seed and straw weight I observed that the yield as seed biomass in the inorganic plots was only significantly higher than the control; and if considering the seed/straw ratio (commonly used for agronomists) there was no difference. These results indicate that inorganically fertilised plots increased the plant biomass, but specifically the straw biomass. My results also reflect that this increase in biomass benefits the herbivore community allowing pests to reach higher levels in inorganically fertilised plots.

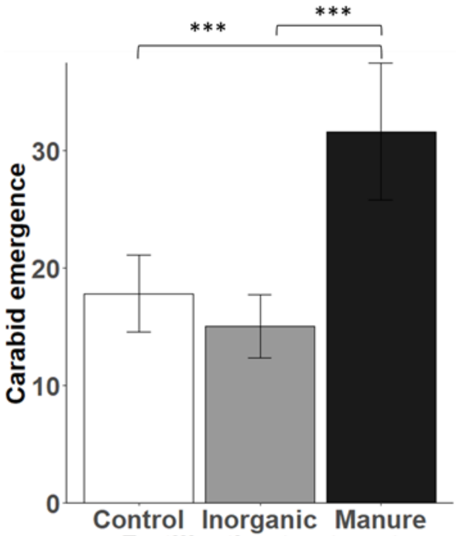


Figure 9. Effect of fertilisation on the emergence of adult carabid beetles from the soil. Average number of adult carabids per treatment and 95% CI. (n=4; *** denotes significant differences P< 0.001). This figure is adapted from paper II.

The final outcome, thus, is that while inorganic fertilisers increase plant biomass, plants also suffer the highest infestation levels. This, level up the final outcome in terms of yield when compared to manure-fertilised plants, that benefits from a more abundant predator community that keep the herbivore damage low. But manure fertilisation benefits other aspects as enriching the overall soil communities and reducing the dependence of crops from external chemical inputs. Thus, these results offer a strong argument toward the use of manure as organic fertilisers.

4.2.2 Predator composition effects

The identity of predators and prey are important to determine the strength in which they interact. In this study, I found that the growth of aphids on the crop plants drastically decreased with the presence of the seven-spotted ladybird beetles, specialised aphid-predators, in the predator community. This result was supported also by the results that showed the strongest top-down control of the aphids in the same communities.

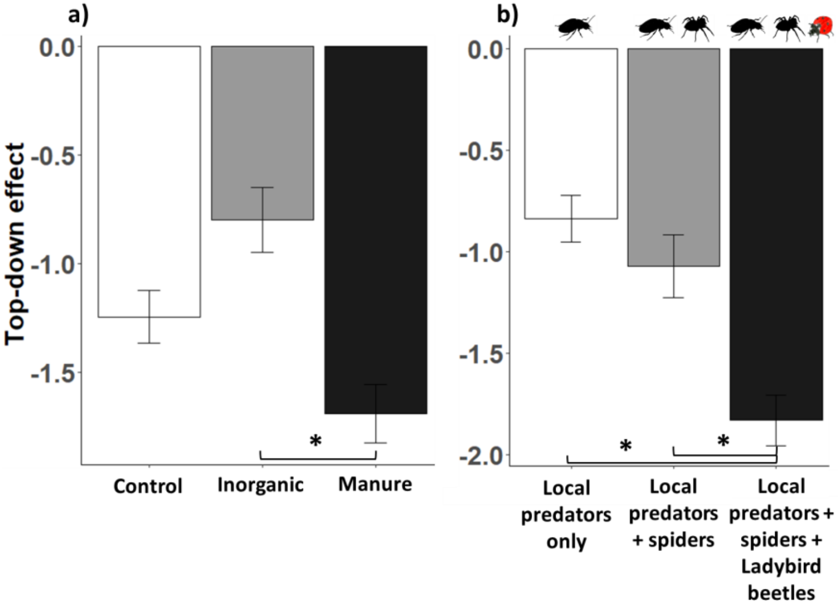


Figure 10. Effect of a) fertilisation and b) predator composition on the suppression of aphids (top-down effects). Average log (Top-down effect) per treatment and 95% CI. (n=4; * denotes significant differences P< 0.01).This figure is adapted from paper II.

This outcome, as mentioned earlier, is a result of a stronger interaction link between a specialised predator and its prey. In this case, it is possible to partially explain such a strong link by identifying predator and prey traits like habitat use. Aphids are most commonly found in high spots on the plant and ladybird beetles are leaf-dwelling predators that have easier access to them than ground-dwelling predators.

However, this design does not allow me to isolate the predation or top-down effect of each predator individually (except for carabids). In other words, we cannot quantify how effective are ladybird beetles alone compared to communities containing also ground-dwelling predators. Aphids can “fall” from the plant to the ground as a defence mechanism when they feel leaf-predators approaching. Thus, if the predator community contains ground-dwelling predators, these could benefit from these mechanisms and increase the predation pressure which would prove a more efficient ecosystem service provision with predator complementarity (Dainese et al., 2017; Gontijo et al., 2015).

4.3 Local and landscape effect on predator-prey food web and their robustness to global changes

Habitat identity had a great effect on shaping the predator communities. In **paper III**, I found clear differences between OSR and ley fields, being the former dominated by a high diversity and abundance of carabid beetles and the later by ground-dwelling spiders. Additionally, a high proportion of OSR in the landscape enhanced carabid diversity and abundances in OSR fields.

When it comes to the robustness of the networks, I found no differences driven by the landscape. However, I found that predator-prey interactions in OSR fields had higher robustness which makes them more stable against changes in the environment. The robustness of these communities was measured upon three metrics that can be associated with the biological control services provided by them (fraction of prey connected, interaction strength and modularity). These results indicate that carabid beetles are well-adapted organisms to agricultural landscapes and highly managed crops. Furthermore, they show a high level of generalisation that converts them into predators of a wide prey spectrum. This level of generalisation creates robust interactions between herbivores.

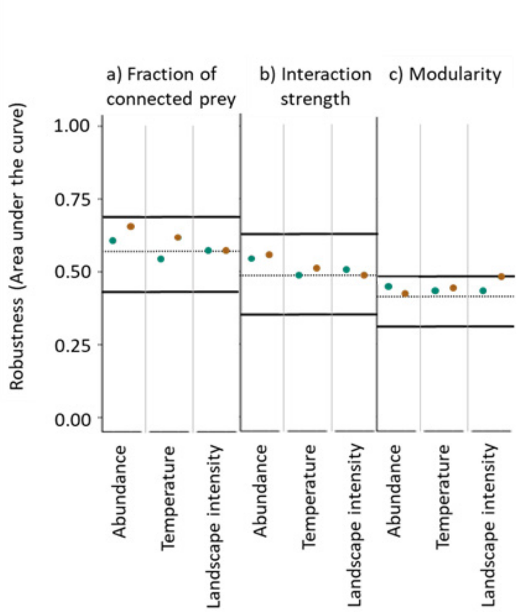


Figure 11. Robustness of predator-prey interaction networks to predator removal measured as the area under the curve for each network metric (sub-figures “a” to “c”). The points represent the mean robustness from the raw data for the three predator removal scenarios based on species traits: abundance, temperature and landscape intensity (x-axis) and crop type (OSR = brown; Ley = green). The upper and lower thick black lines represent the average robustness values under the best and worst removal scenarios. The middle horizontal discontinuous line represents the average robustness value under the random removal scenario. This figure is adapted from paper III.

However, I found that the robustness of a network can drastically change if we define global changes as specific processes and we use species traits to determine the effect of such changes in the species conforming the community. I observed that if predators go extinct as a result of population dynamic processes where rare species go extinct first, we can predict a high robustness of the interactions between predators and herbivores. However, when assessing the effect of climate warming and landscape intensification, as two processes that are rapidly affecting communities around the globe, the robustness of predator-prey interactions decreases. These results suggest that projections of the stability of ecosystem services such as pest control can underestimate the effect of current global changes on the species interaction networks.

4.4 Local and landscape effect on indirect interactions in host-parasitoid food webs

In **paper IV**, I found that host-parasitoid communities were also shaped by both local and landscape factors. Similar to what I observed in the ground-dwelling predator's communities, habitat type had a great effect on the abundance and richness of parasitoids and their herbivorous hosts. In particular, I found the host species richness to be higher in ley habitats than in the OSR crops. Additionally, I observed a marked habitat effect on the species composition since I found that the host community in the ley habitats was clearly dominated by sawflies, while Diptera and Coleoptera dominated the OSR crops. Habitat type also affected the parasitoid community. The molecular analysis of the host species resulted in the identification of 50 parasitoid species in the ley and 17 in the OSR.

Landscape composition affected the assembly of host-parasitoid networks, which resulted in visible effects on the potential for apparent competition among herbivores. Overall, the percentage of annual crops in the landscape reduced the potential for apparent competition in target OSR habitats and increased in target ley habitats. But when only considering non-zero values for apparent competition, I found a decrease in apparent competition when OSR fields are the source habitat and an increase when ley fields are the source habitat.

I also found that attack rates by parasitoids were higher in ley habitats than in the OSR fields. A variance partitioning analysis showed that the between-habitat effect of apparent competition had a stronger influence upon this process than the within-habitat apparent competition. These results support the importance of heterogeneous agricultural landscapes that can enhance the spillover of beneficial arthropods between habitats.

Additionally, I show that we can use apparent competition among herbivores to inform about parasitism rates on specific species. Attack rates for each herbivore species at each site positively correlates with the predicted values only when using the potential for apparent competition, indicating that the indirect interactions have a noticeable effect on the parasitism rates.

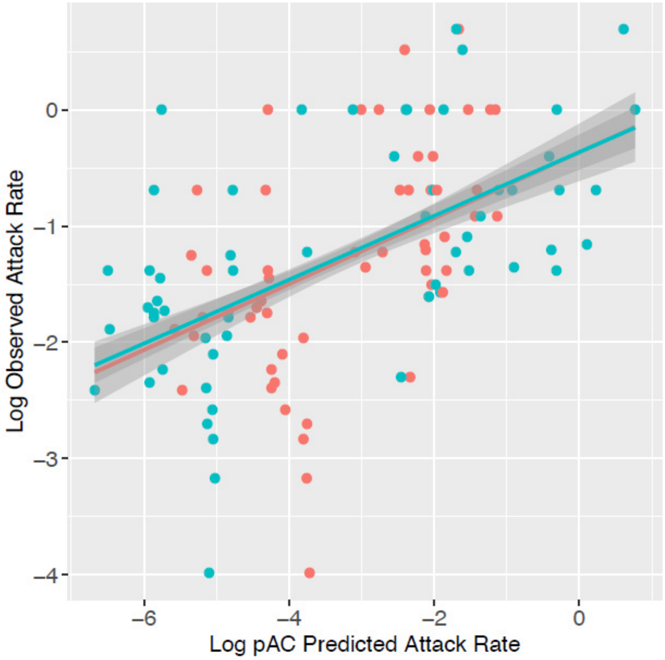


Figure 12. Observed attack rates plotted against predicted attack rates calculated with the natural log of the observed rate of parasitoid attack upon each herbivore host against the natural log of the predicted attack rate. Lines show the model fit where blue indicates rates predicted using the potential for apparent competition between hosts from different habitats and red indicates that between hosts within the same habitat. This figure is adapted from paper IV.

5. Conclusions and future perspective

I show that landscape crop diversity can enhance local communities of predaceous beetles and pollinators in landscapes with a high proportion of semi-natural habitats. Agricultural landscapes are not necessarily homogeneous man-made landscapes and the diversification of agricultural practices seems like a reasonable way to keep producing food without reducing the amount of arable land and enhancing natural enemies and pollinators. Considering these landscapes from a different perspective i.e. considering the resources available to beneficial arthropods, the intensity of their management or their temporal aspect should provide us with a better way to predict the movement of certain species and that can benefit the crop fields with their services.

The influence of the landscape on local communities is inevitably linked to the mobility and dispersion of certain species from source habitats and other types of refuges. However, there is a very limited amount of literature describing the movement of these species across habitats. To really understand the mechanisms of species spillover, directional traps and studies focusing on the movement across fields rather than densities are essential.

I demonstrate that local management, in particular, the use of organic fertilisers can enhance the abundances of local ground-dwelling predators, which is of special interest to provide biological pest control in cases where no other natural enemies move from the surrounding landscape. However, I show that the highest pest control was provided by specialised aphid-predators, seven-spotted ladybird beetles. This result, not only highlights the importance of the spillover of additional predators and other natural enemies from surrounding fields and habitats but also the importance of accounting for the strength of the links between the pest and their consumers. Specialised predators show stronger links with their prey than other predators, which in this case can explain the highest attack rate and predation, and using species interactions is a way to account for these linkages between species.

I present evidence of the utility of species interaction networks (food webs) to understand community assemblages and predict their reaction to possible disturbances and subsequent species extinctions. The robustness of the predator-prey community in OSR fields was greater than in the neighbouring ley fields. Furthermore, I show that the robustness of networks against changes in the environment depends on the type of change. Here, using species traits is a valuable tool to predict how different species will cope with the disturbances, and including a food web approach helps us understand how such changes translate into ecosystems services. In fact, when using species traits I found that the robustness of pest control is lower than what we may expect as a result of extinctions driven by dynamics based on species abundances.

Moreover, I present evidence of “indirect” species interactions as apparent competition being an important part of the ecosystem functioning. I show that apparent competition among herbivorous insects can be measured and used to predict attack rates on specific species. Moreover, the results reveal landscape and local effects in these indirect interactions between species. Concretely, they show that landscape intensification can reduce apparent competition among herbivorous insects. Thus, increasing the proportion of perennial crops such as ley fields can increase apparent competition and raise parasitism levels among pest species.

However, it is not always easy to obtain information about species interaction networks, the sampling effort rapidly increases and in some cases it seems not possible to capture a substantial part of the interactions. Yet, in this thesis, I use molecular tools to characterise predator-prey interactions using the gut of the predators and host-parasitoid interactions using the parasitised host larvae. Molecular tools are currently available and they are becoming cheaper and more accurate. Thus, upcoming research on the field of species interactions should take advantage of these new tools to characterise more realistic food webs.

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Popular science summary

The global decline of insects affect species that are important to humans as providers of key functions in our crops. Wild bees and bumblebees are essential for the pollination of most of the crops with flowers; ground-dwelling beetles or parasitic wasps control pest species, and soil arthropods recycle nutrients. Human activities alter the agricultural landscapes by converting natural habitats into farmland and management practices such as the use of fertilisers can also shape the diversity of species that we can find in a certain crop.

In this thesis, I investigate how landscape composition and local management of crop fields can affect beneficial arthropods inhabiting crop fields and the way they interact with each other. I ask i) how landscape crop diversity affects the diversity of local predators and pollinators ii) how fertilisation affects the local predator community, iii) what the contribution of predators that move from the surrounding landscape into the field is in terms of pest control, iv) and whether we can observe effects of local and landscape land use also on the interaction networks composed of predators and their prey, and parasitoids and their hosts, and v) what the implications are of such effects in the provision of biological pest control.

I found that both landscape composition and local management shape the local arthropod communities of agricultural fields. The diversity of crops in the landscape can increase the diversity of beneficial arthropod species found in the local crop and fertilisation with manure promotes abundances of predatory beetles that suppress herbivore pest species. However, other predators that move from the surrounding landscape, like ladybird beetles, are crucial to suppress certain pest species. The type of crop and the surrounding landscape will thus determine the predator and herbivore species found in the crop. These local and landscape land-use effects also affect the interaction networks. For instance, the predator-prey connections are strong in annual fields, but their stability depends upon the type of global change they face. The landscape management intensity has negative consequences on the indirect interactions between host and parasitoids reducing their potential for pest suppression.

My results suggest that land-use changes occurring at the local and landscape scales affect arthropods and how they interact with each other. Studying both community composition and interaction networks increase our understanding of how environmental changes affect communities and the functions they provide.

Populärvetenskaplig sammanfattning

Den globala nedgången av leddjurer påverkar arter som är viktiga för människor då de levererar avgörande funktioner i våra grödor. Vilda bin och humlor är viktiga för pollinering av de flesta grödor med blommor; marklevande skalbaggar eller parasitiska getingar kontrollerar arter av skadedjur och ryggradslösa djur återvinner näringsämnen. Mänskliga aktiviteter förändrar jordbrukslandskapen genom att omvandla naturliga livsmiljöer till jordbruksmark, och förvaltningsmetoder som användning av gödselmedel kan också forma mångfalden av arter som finns i en viss gröda.

I denna avhandling undersöker jag hur landskapssammansättning och lokal förvaltning av jordbruksfält kan påverka nyttiga ryggradslösa djur som lever i grödor och hur de interagerar med varandra. Jag frågar i) hur mångfalden i landskapet påverkar mångfalden hos lokala rovdjur och pollinerare, ii) hur gödsling påverkar det lokala rovdjurssamhället, iii) vad bidraget från rovdjur som rör sig från det omgivande landskapet in i fältet är för skadedjursbekämpning, iv) om vi kan observera effekter av markanvändning lokalt och i landskapet också på interaktionsnätverken bestående av rovdjur och deras byte eller parasitoider och deras värdar v) vilka konsekvenserna är av sådana effekter för biologisk skadedjursbekämpning.

Jag fann att både landskapssammansättning och lokal förvaltning formar de lokala samhällena av ryggradslösa arter i jordbruksfält. Mångfalden av grödor i landskapet kan öka mångfalden av nyttiga ryggradslösa arter som finns i den lokala grödan och gödsling främjar förekomster av rovlevande skalbaggar som minskar antalet växtätande skadegörare. Men andra rovdjur som rör sig från det omgivande landskapet, som nyckelpigor, är avgörande för att undertrycka vissa skadegörare. Typen av gröda och det omgivande landskapet kommer således att avgöra rovdjur och växtätande arter som man finner i grödan. Dessa effekter av markanvändning lokalt och i landskapet påverkar också interaktionsnätverken. Till exempel är rovdjur-bytesanslutningarna starka i konventionella fält, men deras stabilitet beror på vilken typ av global förändring de möter. Landskapsstyrningsintensiteten har negativa konsekvenser för de indirekta interaktionerna mellan värd och parasitoider, vilket minskar deras potential att öka skadedjursundertryckningen.

Mina resultat tyder på att förändringar i markanvändning som sker på lokal och landskapsskala påverkar ryggradslösa djur och hur de interagerar. Att undersöka både samhälls-sammansättning och interaktionsnätverk ökar förståelsen för hur förändringar i miljön påverkar organismsamhällena de funktioner de tillhandahåller.

Resumen de divulgación científica

El declive global de insectos afecta a especies que son fundamentales para los humanos como proveedores de funciones vitales para nuestros cultivos. Las abejas silvestres y los abejorros son esenciales para la polinización de la mayoría de los cultivos de plantas con flores; ciertos escarabajos o avispas parásitas controlan especies que pueden llegar a convertirse en plagas; y muchos de los invertebrados que habitan suelo tienen un papel fundamental en el reciclaje de nutrientes. Sin embargo, las actividades humanas alteran los paisajes agrícolas al convertir los hábitats naturales en tierras de cultivo y prácticas agrícolas como el uso de fertilizantes también pueden afectar a la diversidad de especies que podemos encontrar en un determinado campo de cultivo.

En esta tesis, investigo cómo la composición del paisaje y las prácticas agrícolas locales pueden afectar a los invertebrados beneficiosos que habitan los campos de cultivo y la forma en la que interactúan entre sí. Para ello me pregunto i) ¿Cómo afecta la diversidad de cultivos en el paisaje a la diversidad local de depredadores y polinizadores? ii) ¿Cómo afecta la fertilización a la comunidad local de depredadores? En términos de control de plagas, iii) ¿Cuál es la contribución de los depredadores que migran al campo de cultivo desde el paisaje circundante? iv) ¿Podemos observar efectos locales y paisajísticos también en las redes de interacción de especies compuestas por depredadores y sus presas o parasitoides y sus hospedadores? y v) ¿Cuáles son las implicaciones de tales efectos en la provisión de control biológico de plagas?

Observé que tanto la composición del paisaje como las prácticas agrícolas locales dan forma a las comunidades de invertebrados locales de los campos agrícolas en diferentes niveles. La diversidad de cultivos en el paisaje puede aumentar la diversidad de especies de invertebrados beneficiosos que se encuentran en determinado campo de cultivo y la fertilización con estiércol promueve una mayor abundancia de escarabajos depredadores que ayudan a suprimir plagas de herbívoros. Sin embargo, otros depredadores que migran al campo de cultivo desde el paisaje circundante, como las mariquitas, son cruciales para reprimir ciertas especies de plagas. Así pues, el tipo de cultivo y el paisaje circundante determinarán las especies de depredadores y herbívoros que se pueden encontrar en él. Sin embargo, estos efectos locales y paisajísticos también son visibles en las redes de interacción entre especies. Por ejemplo, las interacciones depredador-presa son más fuertes en los campos de cultivo anuales, pero su estabilidad depende del tipo de cambio global al que se enfrenten (aumento de las temperatura, aumento de la intensidad agrícola, etc.). El nivel de intensidad de las prácticas agrícolas del paisaje circundante tiene efectos negativos en las interacciones indirectas entre insectos herbívoros y sus parasitoides, lo que reduce su potencial para aumentar la supresión de plagas.

Estos resultados sugieren que los cambios que ocurren a escala local y de paisaje afectan a los invertebrados y la forma en que interactúan. Por lo tanto, además de la composición de especies, el estudio de las interacciones entre especies es una herramienta poderosa para comprender cómo reaccionan las comunidades a los cambios derivados de las actividades humanas y cómo las funciones importantes proporcionadas por esas especies se pueden ver afectadas por tales.

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