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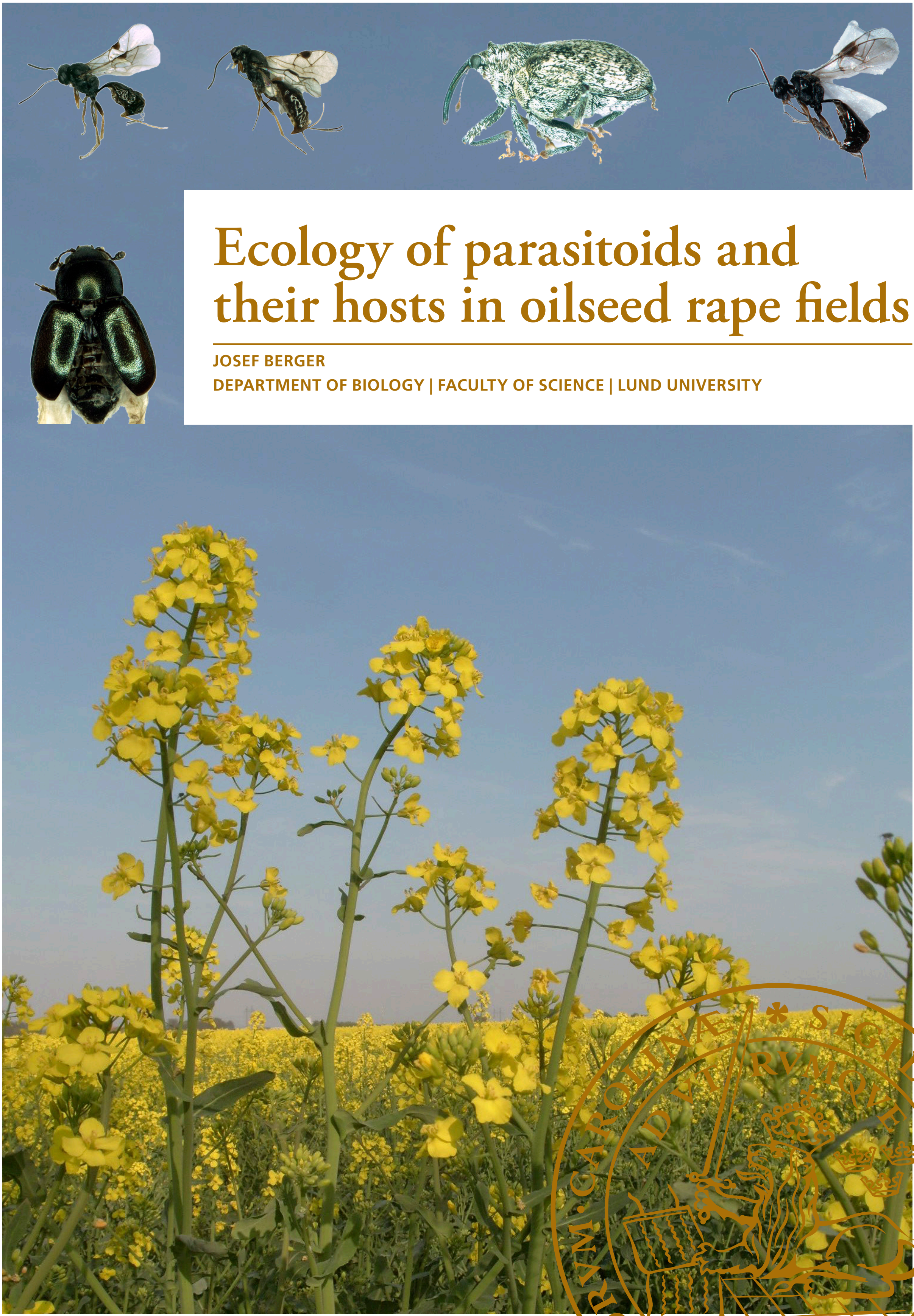

Ecology of parasitoids and their hosts in oilseed rape fields

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Ecology of parasitoids and their hosts in oilseed rape fields

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Josef Berger

LUND
UNIVERSITY

DOCTORAL DISSERTATION

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Abstract

Oilseed rape fields are a very common crop in the agricultural landscape of southern Sweden, and they can harbour surprisingly many insect species. Some of them are herbivores that feed on various parts of the oilseed rape plant, others are natural enemies of the herbivores, and even more species are tourists from the surrounding landscape. In my thesis I have studied these insects and how their presence/absence and abundances can be explained by ecological processes.

This thesis addresses the following questions: How do pollen beetle parasitoids avoid competition while sharing the same host species? Do parasitoids of the cabbage stem weevil use the landscape on a smaller scale than their host? How does agricultural landscape configuration affect the community composition and potential interaction networks of herbivore and parasitoid communities? What is the relative contribution of niche assembly and dispersal assembly to empirical species abundance distributions of parasitoids and beetles?

I found evidence for both temporal, spatial and behavioural niche separation between pollen beetle parasitoids: All three studied parasitoid species use odours for host location, but they differ in timing, host stage preference and host microhabitat preference.

Although ecological theory expects parasitoids to use landscape on a smaller scale than their hosts because of a smaller body size and extreme specialisation, I found no support for this expectation in the parasitoids of the cabbage stem weevil: While habitat proportion at the 1 km scale was the most important predictor for abundances of the cabbage stem weevil, this scale did not matter for both its parasitoid species, whose abundances were best explained by pesticide application and host abundance (in *Tersilochus obscurator*), or host abundance only (in *Stibeutes curvispina*), regardless of scale. Probably they utilise the landscape on a larger functional scale than their host.

On community level, the presences and absences of several parasitoid species and host species were affected by several landscape variables: Distance from the collection site to forested land, and oilseed rape within a 1 km radius, was an important predictor of variation in community composition. Host-parasitoid interaction networks became more asymmetrical with increasing distance from forests, due to relatively fewer pest than parasitoid species. Consequently, growing oilseed rape in regions that are situated far away from forests is likely to minimize recolonization by pest species and at the same time to attract more parasitoid species from the open landscape.

The variation in both parameters of parasitoid species abundance distributions was significantly affected by environmental variables, but not by geographical distance. From this, we conclude that parasitoids in the metacommunity have sufficiently high dispersal rates to track environmental variation between the local sites. In contrast, there was no effect of environmental variables on beetle species abundance distributions, but beetle commonness was dependent on geographical distance between sites, which was most pronounced at the 4-6 km scale. This indicates that the most common beetle species in oilseed rape fields are stronger affected by geographical proximity than the most common parasitoid species.

Taken together, the results of my thesis suggest that parasitoid wasps in the oilseed rape habitat can disperse over larger distances than what was previously thought. Hence, there is a need for large-scale perspective on parasitoid abundances that reaches beyond a few kilometres, if we want to promote the persistence and the diversity of parasitoid wasps in the agricultural landscape..

Key words
Parasitoids, herbivores, oilseed rape, pollen beetle, cabbage stem weevil, niche separation, landscape scale, community composition, landscape configuration, species abundance distribution, dispersal

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Till mina barn,
som inte fanns när jag började doktorera,
men som redan nu vet mer om insekter
än jag när jag var i deras ålder.

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Paper II

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Author contributions

Paper I

JB and MJ developed the research questions with contributions from PA and KH. JB and MJ grew the plants. JB did the laboratory bioassays and quantified the phenology. MJ did the outdoor bioassays and the field observations. JB and MJ did the statistical analysis and wrote the manuscript with contributions by KH and PA.

Paper II

JB developed the research questions with contributions from KH. JB, HH and KH set up the study design. JB and HH did the field work. JB did the laboratory work and the species identifications, processed the data and did the statistical analysis. JB wrote the manuscript with contributions by KH, HH and PA.

Paper III

JB and KB developed the research questions. JB, HH and KH set up the study design. JB and HH did the field work. JB did the laboratory work and the species identifications and processed the data. KB did the statistical analysis. JB wrote the manuscript with contributions by KB, KH and HH.

Paper IV

JB developed the research questions. JB, HH and KH set up the study design. JB and HH did the field work. JB did the laboratory work and the species identifications, processed the data and did the statistical analysis. JB wrote the manuscript with contributions by KH, PA and OA.

Introduction

Biodiversity

One of the major aims of ecology is to understand the changes of biodiversity in space and time. Biodiversity can be broadly defined as "the variety of life, at all levels of organization" (Colwell 2009), but often it is understood more narrowly as species richness and relative species abundance in space and time (Hubbell 2001). The observed variation in diversity between different communities has been variously explained with theoretical frameworks such as interspecific competition (Hutchinson 1959), environmental parameters (Whittaker 1972), dispersal (MacArthur & Wilson 1967, Hubbell 2001) and metacommunity dynamics (Holyoak et al. 2005). In this thesis, I try to integrate all of them.

About half of all known multicellular species on this planet are insects (Zhang 2013, Catalogue of Life 2017). Consequently, the recently noticed worldwide decline in insect biodiversity (Sánchez-Bayo & Wyckhuys 2019) is alarming, since we can expect profound effects on food webs, ecosystem functioning, and the ecosystem services that insects provide to humanity. Analysing insect abundances in order to find out what affects them is thus an essential task. I have therefore chosen in my thesis to study the ecological processes which affect insect abundances and community composition in agricultural ecosystems.

Agricultural ecosystems

It has long been known that a large part of terrestrial biodiversity exists in human-managed ecosystems (Pimentel et al. 1992). About half of Europe is covered by agricultural landscape, and many species have adapted to habitats connected with traditional agricultural practices in the centuries before the advent of new production methods (Tscharntke et al. 2005a). However, the need to feed the growing human population has during the past decades led to an intensification of agriculture (Tilman et al. 2011, Tscharntke et al. 2012), and consequently, the agricultural landscape of Europe has dramatically changed: What was previously characterized by mosaic landscapes consisting of small fields and pastures interspersed with various non-crop habitats (e.g. hedgerows, fallows, woodlands), has since the mid-1960s been transformed into increasingly homogeneous landscapes through expansion of total agricultural area, increase of individual field size, plantation of genetically uniform monocultures, and elimination of non-crop elements to facilitate mechanization (Robinson & Sutherland 2002, Bianchi et al. 2006, Lemaire et al. 2017). There is a growing consensus that this homogenization of landscapes, together with the excessive use of agrochemicals such as synthetic fertilizers and pesticides per unit area, leads to a general decline in farmland biodiversity (Emmerson et al. 2016) and the associated ecosystem services provided e.g. by pollinators (Le Féon et al. 2010, Bommarco et al. 2012), nutrient recyclers (Losey & Vaughan 2006) and natural control agents (Bianchi et al. 2006, Chaplin-Kramer et al. 2011). Advancing our knowledge about ecological processes and biodiversity in agroecosystems is therefore necessary for the development of specific habitat management strategies to suppress densities of crop-feeding herbivores and to support their natural enemies and other beneficial arthropods (Landis 2017, Gurr et al. 2017).

Pests and parasitoids

Insects that feed on agricultural crops are commonly termed "pests", which reflects their negative impact on food production; sometimes literature differentiates between major pests and minor pests, reflecting their economical significance (Alford et al. 2003). Since the same species may be classified as major pest, minor pest, or even irrelevant depending on continent and country, I prefer the less negatively connotated term "herbivores". Herbivorous insects in the agricultural landscape may be adult feeders or larval feeders, and they may be specialised on various nutritious resources provided by the plant (pollen, leave tissue, stem or petiole tissue, root tissue or phloem sap). Each of them has a multitude of natural enemies, but in this thesis I restrict the focus on parasitoid wasps.

Parasitoid wasps are insects of the order Hymenoptera that share a particular lifestyle: They oviposit into or on a developmental stage of an arthropod host (often the egg or larva) and, after hatching, the parasitoid larva feeds on the host and ultimately kills it (Gauld & Bolton 1988). Prior to oviposition, the host selection behaviour of parasitoids consists of host habitat location, host location, host recognition and host acceptance (Vinson 1976). The host habitat is often located by using highly volatile chemicals as long-distance attractants, often odours that are emitted by plants specifically as a response to herbivory (Turlings & Erb 2018). There is field evidence that parasitoids are able to fly upwind to locate their host habitat (Williams et al. 2007). After localising the host plant and landing on it, the parasitoid female walks around until it encounters its host - a behaviour which was called random searching by many early authors, but which can be better understood as using olfactory, gustatory, or visual senses (Vinson 1976, 1998). Particularly for parasitoids whose females have purportedly a limited life span of less than a week during summer (Nilsson 2003), there should be some selective pressure for not wasting time by random walking if there are useful physical or chemical cues. For this reason, **paper I** examines the preference behaviour of three parasitoid species for volatile cues from uninfested and infested plant parts, and from the larval host.

Parasitoid wasps are megadiverse, with 60,000 described and about 630,000 estimated undescribed species (Heraty 2009) and there is incontestable evidence that they can have profound impacts on their host populations (Shaw & Hochberg 2001). However, the biology of most of these species is unknown or very poorly studied (Huber 2009), which may be attributed to their often small size and the lack of taxonomic expertise. Despite our lack of knowledge, these insects are far from negligible for human welfare: The economical value of pest control attributable to predators and parasitoids in the United States has been recently, in a very conservative calculation, estimated at approximately 4.5 billion USD annually (Losey & Vaughan 2006). It is not surprising that the largest bulk of ecological literature concerns those parasitoid species which parasitise major agricultural "pests". Nonetheless, even for those species, our knowledge is limited and various studies of the same host-parasitoid species system in different countries have arrived at different conclusions (Zaller et al. 2008, Schneider et al. 2015, Hanson et al. 2015). **Papers I** and **II** focus therefore on the autecology of parasitoids of two of the most abundant "major pests" of the studied agricultural system. **Papers III** and **IV** have a broader scope, as they analyse entire communities: In **paper III**, the focus is on qualitative community composition and host-parasitoid interactions, and in **paper IV** on the species abundance distributions of beetles and parasitoids.

Study system

In all four papers, I have studied the tritrophic ecosystem oilseed rape - herbivores - parasitoids.

Oilseed rape, *Brassica napus* L. (Brassicaceae), is an important agricultural crop plant in Europe, grown for its seedpods which are crushed to extract oil (Alford 2003). In contrast to summer oilseed rape which is sown in the spring and common in central Sweden and Finland, this study deals entirely with winter oilseed rape which is the most common brassica variety grown in southern Sweden: It is sown in autumn, germinates and develops leafs before overwintering, followed in the spring by stem elongation, bud growth and flowering (usually in May) (Fig. 1) and seedpod maturation (usually in June). In order to minimise the buildup of soil pathogens and the depletion of nutrients, winter oilseed rape is not grown in the same field every year, but in rotation with cereals; in this this part of Sweden, it is traditionally grown in the sequence barley - winter oilseed rape - winter wheat - sugar beet, but there exist also other sequences (Wikström 1997).

Figure 1:
Flowering oilseed rape at Lönnstorp in May 2011.

Paper I and **paper II** focus on two of the most abundant herbivorous beetles in Swedish oilseed rape fields, and the ichneumonid wasps that parasitise them. Both beetle species (Fig. 2) share some aspects of their life cycle: Adult beetles migrate from their overwintering sites (under leaf litter at the edges of woods or shrubs) into the oilseed rape fields early in the spring (Günthart 1949). The larvae of both beetles feed in different microhabitats of the plant, but in both species the mature larva actively drops from the plant in order to pupate in the soil. After metamorphosis, the next generation of beetles emerges a few weeks later; however, if the host larva was successfully parasitised and killed by an ichneumonid parasitoid, then this parasitoid overwinters as diapausing adult inside the pupal cocoon of the host and emerges in the subsequent spring. Since these parasitoid species are numerically of highest relevance for natural control of their hosts, improving our knowledge of their biology might be beneficial for the development of organic management strategies for oilseed rape crops.

Figure 2:
a) The pollen beetle, *Brassicogethes aeneus* (Nitidulidae: Meligethinae). b) The cabbage stem weevil, *Ceutorhynchus pallidactylus* (Curculionidae: Ceutorhynchinae).

The pollen beetle *Brassicogethes aeneus* (Fabricius, 1775) (Nitidulidae: Meligethinae) is considered by Swedish oilseed rape farmers as their most serious enemy. After emergence from overwintering and a brief polyphagous phase on wild plants, it arrives in the oilseed rape fields in order to oviposit, and there it makes most damage to the crop when adults feed on the pollen in green buds prior to oviposition (Mauchline et al. 2018). Pollen beetle larvae develop in the buds and the flower, feeding on pollen, until they drop from the plant in order to pupate in the soil. The three most common parasitoids of the pollen beetle are *Tersilochus heterocerus* (Thomson, 1889) (Fig. 3), *Phradis morionellus* (Holmgren, 1860) and *Phradis interstitialis* (Thomson, 1889) (Ichneumonidae: Tersilochinae). In this study region, all three species have been reported to occur together in winter oilseed rape (Jönsson et al. 2004), which is why I have studied their niche separation in **paper I**.

The cabbage stem weevil *Ceutorhynchus pallidactylus* (Marsham, 1802) (Curculionidae: Ceutorhynchinae) feeds on leaves and oviposits into petioles and midribs of the plant (Günthart 1949). Two of its most abundant parasitoids are *Tersilochus obscurator* (Aubert, 1959) (Ichneumonidae: Tersilochinae) and *Stibeutes curvispina* (Thomson, 1884) (Ichneumonidae: Cryptinae). As very little is known about the biology of these two species (particularly of the latter) and landscape ecology studies are completely lacking, I chose this host-parasitoid system to test predictions about the relative spatial scale required by parasitoids and their respective host species in **paper II**.

Figure 3:
Tersilochus heterocerus (Ichneumonidae: Tersilochinae), one of the key parasitoids of the pollen beetle.

Oilseed rape fields are complex habitats that harbour many other insect species (**papers III** and **IV**). **Paper III** focuses on the species composition of those parasitoid and host species that were found in each site and can be linked to each other and to the oilseed rape habitat based on published host records. (For time reasons, I constrained the analysis to herbivorous Coleoptera and Heteroptera, and their respective parasitoids.) In addition to species composition, **paper III** also analyses the interaction networks which result from this potential linkage.

Paper IV takes the most general biodiversity approach and compares different theoretical species abundance distributions, calculated from the abundances of all parasitoid species and all herbivorous beetle species that were collected in the study sites and that I was able to identify.

Theoretical frameworks explaining biodiversity patterns

Competition

In order to explain why certain species are common (i.e. occur in high abundances) and other species are rare (i.e. occur in low abundances), competition for limited resources tends to be the first explanation that comes into an ecologist's mind. Competition between species has long been viewed as the most important factor that structures ecological communities (Connell 1983, Schoener 1983). Competition theory predicts that two or more species cannot coexist when competing for a single limited resource (Hardin 1960, Meszéna et al. 2006, Kalmykov & Kalmykov 2013). In order to avoid competitive exclusion, species with similar resource requirements are expected to differentiate their niches (Chesson 2000). The differentiation of resource utilisation in two species due to competition pressure was termed "character divergence" by Darwin, but since the development of the ecological niche concept it is more known as "niche separation" (den Boer 1986). If one imagines a species' niche as a multidimensional hypervolume (Hutchinson 1957), then niche separation can happen by diverging along one or more of its axes, for example resource utilisation, space and time (Amarasekare 2003). **Paper I** provides evidence about niche differentiation among three closely related parasitoids of the pollen beetle, in order to explain how they can coexist in the same habitat sharing the same host.

Landscape ecology

Agricultural crops can be seen as a very dynamic ecosystem, since they are present only for a brief period of the year and are commonly grown in rotation - i.e. they are neither constant in time nor in space. Furthermore, soil perturbation by machines and excessive use of insecticides can be seen as potent mortality factors. Consequently, the agricultural field is a quite hostile environment to live in. The population dynamics of organisms in an agricultural ecosystem can therefore be understood in terms of local extinctions and colonizations from the surrounding landscape, thus implying source-sink population structures (Pulliam 1988). In such a system, a specialist species can persist by a mass effect in one site because of a high colonization rate from other sites (Holt 1993), while a generalist species can persist by having access to multiple habitats in the landscape (van Nouhuys & Hanski 2002).

Many ecological processes (e.g. foraging, dispersal, metapopulation dynamics) operate on larger scales than single fields and farms, since many organisms are capable of active movement (Smith et al. 2014). A landscape perspective on ecological processes views the involved organisms in the context of the landscape surrounding the sampling site, taking into account the composition of local characteristics and the spatial pattern of habitat elements (Roland 2000). However, it is not well understood how populations of natural enemies of agricultural pests react to specific landscape elements (Bianchi et al. 2008). **Papers II, III and IV** deal specifically with the relative contributions of various elements of the agricultural landscape and local management to different response variables of herbivores and parasitoids.

Spatial scales

Many arthropods that are commonly found in the agricultural landscape are capable to disperse over distances ranging from a few hundreds of metres (Alford et al. 2003) to tens of kilometres (Hastings 2000). Species which have wings can generally be assumed to disperse primarily by active flight, passive aerial dispersal, or a combination of both (Compton 2002). Consequently, the dispersal capacity of an organism may depend on its size, wing morphology and associated physiological species-specific traits (Asplen 2018). It is common that landscape ecologists infer dispersal capacity indirectly from the "functional spatial scale", which an organism utilizes in order to successfully complete its life cycle. This functional spatial scale can be determined by spatial regression techniques: These are based on how the effect of habitat elements changes when a response variable is measured at different spatial scales (Roland 2000, Thies et al. 2003, Thies et al. 2005). The spatial scale at which the studied organism responds to its landscape context is often interpreted as indicative of the dispersal capacity of this organism, but it may just as well represent the optimal foraging range of the species, given a particular landscape configuration.

Seen from the niche perspective, different species in the same community occupy different ecological niches and they may have different spatial requirements in order to complete their life cycle. Robert Holt has developed a theoretical framework for community ecology in which organisms on different trophic levels experience landscape on different scales, depending on their trophic rank, degree of specialization, body size, and mobility (Holt 1996, Holt et al. 1999, Holt et al. 2005). In this theory, large-sized animals are predicted to respond to habitat elements on larger spatial scales than smaller animals; small-sized trophic specialists, such as parasitoids, are predicted to experience smaller spatial scales than their hosts. In **paper II**, I test the predictions of Holt's theory for two different trophic levels (a herbivorous host and its parasitoids).

Community composition and interaction patterns

On community level, species richness (i.e. the number of species in a site) is still the most common way to measure biodiversity; being a discrete number, it is the most straight-forward concept, as it can easily be grasped even by journalists, politicians, and decision takers. However, to fully understand processes that structure communities, it is necessary to take into account also species identity and community composition (Symstad et al. 1998, Emery & Gross 2007). In recent years, there is also a growing awareness that the traditional concept of biodiversity needs to be widened to encompass even the diversity of interactions between species, since there is an increasing amount of work showing that the structure of interaction networks affects ecosystem stability (Tylianakis et al. 2010, Miranda et al. 2013). In **paper III** of this thesis, I have therefore studied species identity and the composition of host and parasitoid communities with multivariate analysis, and also calculated two metrics which are based on species richness but characterize interaction networks in every host-parasitoid system: Web asymmetry and linkage density. Web asymmetry (also known as matrix shape) indicates the topology of the trophic network and tells us whether it is dominated by the number of higher trophic level species or by the number of lower trophic level species (Blüthgen et al. 2008, Ulrich 2009). Linkage density is a metric of the complexity in a trophic network; it is calculated by dividing the number of interactions (i.e. host-parasitoid links) by the number of nodes (i.e. interacting species) in the network (Miranda et al. 2013).

Commonness and rarity

Patterns of commonness and rarity of species have been fascinating biologists since Darwin (1859), who noted that "rarity is the attribute of a vast number of species of all classes, in all countries". Indeed it is a universal property of all ecological communities that many species are rare and only a few species are very common (Kunin & Gaston 1993, McGill et al. 2007). Species abundance distributions (SADs) are a way to analyse multiple aspects of biodiversity by providing a quantification of species abundances of an entire assemblage collected at a site and characterising its particular pattern of common and rare species (Foster & Dunstan 2010, McGill 2011, Matthews & Whittaker 2014). The recent acceleration of computationally intensive calculations makes it now possible to compare species abundance distributions by rigorous statistical testing (Connolly et al. 2009, Connolly & Dornelas 2011) in order to explain systematic patterns in relative species abundances with their environmental correlates (Fattorini et al. 2016, Ulrich et al. 2016). For example, patterns in species abundance distributions have been used to detect effects of anthropogenic impact on biodiversity (Dornelas et al. 2009, Simons et al 2017, Komonen & Elo 2017). In **paper IV**, I apply species abundance distribution modeling to parasitoid and beetle communities in oilseed rape, in order to test which ecological processes structure their community assembly.

Community assembly

Competition for limited resources constitutes the theoretical narrative behind most classical species abundance distribution models (Wilson 1991). In the classical "niche-assembly perspective" (a term coined by Hubbell 2001), ecological communities are viewed as limited-membership assemblages of species which have partitioned the available niche space and coexist at an adaptive and demographic equilibrium; their species abundance distributions are determined by the environmental attributes, individual species traits, and interspecific competition for limited resources. The past decades have, however, challenged this view with an alternative explanation which puts more weight on the role of dispersal, i.e. the movement of individuals from one site to another (Holyoak et al. 2005): The "dispersal-assembly perspective" sensu Hubbell (2001) views ecological communities as open, permanently changing, nonequilibrium assemblages which are a dynamic result of chance, history, and geography. Under the extreme assumptions of neutral theory (in which environmental differences and species traits are irrelevant), dispersal-assembled species abundance distributions are thus largely driven by stochasticity and events of local extinction and colonization (Hubbell 2001, Alonso et al. 2006, Wennekes et al. 2012). In **paper IV**, I have analysed the relative contributions of niche assembly and dispersal assembly to empirical abundance data on local community level and on metacommunity level.

A metacommunity can be understood as a set of local communities that are linked by the dispersal of one or more of their members (Holt 1997). Modern metacommunity theory (Leibold et al. 2004, Holyoak et al. 2005) attempts thus to integrate both niche-based and dispersal-based dynamics into a common framework, acknowledging that any local community is likely to be determined by both local processes (e.g. environmental parameters and species interactions) as well as regional processes that operate on larger scales (such as dispersal patterns).

In the past 15 years, community assembly processes have often been classified as one of four metacommunity paradigms - patch dynamics, species sorting, mass effects and neutrality (Leibold et al. 2004, Holyoak et al. 2005). However, these four historical paradigms are neither mutually exclusive (Logue et al. 2011), nor do they represent the full inference space of metacommunity theory, which is continuous and multidimensional (Brown et al. 2017). While the neutrality paradigm ignores local site quality and interspecific differences and assumes a probabilistic colonisation of sites regardless of species identity (Hubbell 2001), the other three metacommunity paradigms all allow for interspecific competition (i.e. they start from the niche-assembly perspective) but put different emphasis on local site quality, heterogeneity, and dispersal rate. Recently, it was pointed out that both patch dynamics and mass effects can be understood as special cases of species sorting, with the main distinguishing feature being the amount of dispersal between communities (Winegardner et al. 2012). All three non-neutral paradigms can be simultaneously applied to the same metacommunity, as illustrated by the following model from Heino et al. (2015), in which geographical distance between local communities is viewed as an indirect surrogate for relative dispersal rate (with spatial proximity indicating high dispersal and large distances low dispersal): If sites are close together, high dispersal has a homogenizing effect on community structure regardless of local environmental factors (mass effect), whereas intermediate distances between sites allow species to effectively disperse and experience variation in local environments (species sorting) and very long distances between sites permit only limited dispersal, so that some species are missing from suitable sites because local extinction is not compensated by recolonisation (patch dynamics). For these reasons, it can be informative to study the effects of environmental factors and geographical distance on the same response variable; and this is what I did in **paper IV**, by studying the variation in empirical species abundance distribution patterns between 21 local communities on two trophic levels. In the same paper, I have also tested whether a decomposition of the metacommunity into "residents" (i.e. species that are associated with the particular habitat type of the study) and "tourists" (i.e species that have no known association with the habitat) can disentangle niche assembly processes and dispersal assembly processes: Theoretically, the residents of a habitat may be structured by competition for available resources (and thus their species abundance distribution may fit mathematical models based on competition theory), while occasional immigrants from outside the habitat may be structured by stochasticity (and thus their species abundance distribution may fit mathematical models based on neutral theory).

Aims

On *autecology level*, this thesis addresses the following general questions:

● How do sympatric parasitoids of the same host species avoid competitive exclusion? Parasitoid wasps that attack and develop in the same host species must necessarily experience either exploitative or interference competition (Mills 2003) and therefore need to differentiate their realised niches in order to coexist. **Paper I** provides evidence on how niche differentiation is accomplished among three pollen beetle parasitoids (*Tersilochus heterocerus*, *Phradis interstitialis* and *Phradis morionellus*).

● Do parasitoids use the landscape on a smaller scale than their host? Due to their small body size and extreme specialisation, parasitoids are expected to use the landscape on a smaller spatial scale than their adult hosts which are larger and therefore expected to have a larger foraging range (Tscharntke & Brandl 2004, Holt et al. 2005). In **paper II**, I have analysed this prediction on the abundances of the cabbage stem weevil and two of its ichneumonid parasitoids, *Tersilochus obscurator* and *Stibeutes curvispina*. In the same paper, I have also tested whether parasitoids are more sensitive to insecticide residues than their host, and whether the two ichneumonids have similar phenology and landscape requirements.

On *synecology level*, this thesis addresses the following general questions:

● How are species composition of multiple parasitoid and host communities and their interaction networks affected by agricultural landscape variables? In **paper III**, I have tested the hypothesis that variation in species composition (expressed by presences and absences of species per site) and network topology depends on (1) the proximity of hibernation sites (woody areas for hosts, and sites where oilseed rape was grown in the previous year for parasitoids), and (2) on habitat area.

● Which model does best predict empirical species abundance distributions of parasitoids and beetles in oilseed rape? And what is the relative contribution of niche assembly and dispersal assembly to empirical patterns of commonness and rarity on local community level and on metacommunity level? If niche specificity is important for patterns of commonness and rarity, then we expect that the species abundance distribution parameters should depend on variation in environmental factors. If dispersal limitation is important for patterns of commonness and rarity, then we expect that the variation in model residuals should depend on geographical distance. If we find no effect of environmental factors on the species abundance distribution parameters, then dispersal limitation may be seen as sufficient explanation for patterns of commonness and rarity. (**Paper IV**)

Methods

Study region

All work for this thesis was carried out in the agricultural landscape between Lund and Malmö in southern Sweden, which is characterized by a high proportion of arable land (on average 85.5% within a 1000 m radius around each study site), dominated by winter wheat, winter oilseed rape, spring barley and sugar beet (see Tab. S1 in **paper IV**).

Experimental design

The field data for this thesis were collected during the time when oilseed rape develops from the bud stage to seedpod maturation.

The field data for **paper I** were collected at the Lönnstorp experimental farm, owned by the Swedish Agricultural University Alnarp (N55° 40.15' E13° 06.51'), between 4 May and 21 June 2011 and between 30 April and 19 June 2012.

The field data for **papers II, III, IV** were collected at 26 winter oilseed rape fields owned by local farmers in the study landscape (see Fig. 1 in **paper III**), between 11 May and 21 June 2010. The sites were selected according to their distance from fields where oilseed rape was grown in the year before: This was either directly adjacent (in a distance of 30 m), or not adjacent (in a distance ranging between 375 m and 1061 m). A second criterion for site selection was a variable proportion of oilseed rape within a radius of 1 km around the sampling site (between 0.0 and 33.5% in the year before the study, and between 2.2 and 30.9% in the study year).

Information about agricultural land use was obtained from the Integrated Administration and Control System (*Blockdatabasen*) of the Swedish Board of Agriculture, an annually updated database of spatially explicit data on crop area and other land use reported by the farmers. All geographical distances (i.e. distances between sites, and distances between each collection site and the nearest forest margin) were calculated with ArcGIS software 9.3 and 10.0, based on the general map of the study region provided by the Swedish National Land Survey (*Lantmäteriet*).

Based on a questionnaire sent to the local farmers who owned the fields, we know that 8 of the 26 fields were treated with various insecticides in late April or early May (see details in **paper III**) and 13 were not treated. Unfortunately, information about insecticide application was impossible to obtain for five of the 26 sites for various reasons, including death of the farmer. The difference in qualitative community composition between the 8 treated and the 13 untreated fields turned out not to be statistically significant (see details in **paper III**), and so the five fields with uncertain insecticide status were included in the analysis of **paper III**. However, for the analysis of abundance data in **papers II** and **IV**, I chose to exclude the five sites with uncertain insecticide status from the analysis, thereby reducing the sample size to N=21 fields.

Paper III had thus the largest sample size (N=26) but the first collection week was excluded from the analysis, since not all sites could be sampled already on the first day. It took several days to place all traps around the landscape, and therefore the first collection week does not cover all 26 sites. After exclusion of the first collection week, the total collection time span of **paper III** is 30 ± 2 days, and the same time period was chosen for analysis in **paper IV**. In contrast, the first collection week was included in **paper II**, because there I studied the relative phenology of three insect species over time and therefore their relative abundances during the first week were very relevant as well (see Fig. 6 in **paper II**). The unequal number of collecting days per site was therefore added as a local covariate into the abundance analysis in **paper II**.

Insect collection

Oilseed rape plants for the bioassays in **paper I** were transplanted from the soil into pots at the Lönnstorp field in March 2012, prior to the arrival of pollen beetles. I selected only such plants at the beginning of stem elongation which had not yet developed any flower buds. The plants were grown in the greenhouse until they reached flowering stage.

Insects for the bioassays in **paper I** were collected in 2011 and 2012 at the Lönnstorp experimental farm: Pollen beetle eggs were collected by dissection of infested oilseed rape buds from the same field. Pollen beetle larvae and parasitoids were swept from the plants with a sweepnet and collected with an aspirator. Living parasitoids were kept indoors at 12°C in ventilated plastic boxes with wet tissue paper. A freshly cut oilseed rape inflorescence, some drops of water, and fresh honey were added twice a week. The parasitoids were tested within 1-2 weeks after collection.

The insect data for **Papers II, III, IV** were collected at each site in 3-5 transparent plastic trays, located on the soil and placed into the oilseed rape field at a distance of 30 m from a field edge, not bordering another oilseed rape field in the same year. The replicated trays were separated by approximately 20 m from each other. Each tray captured a surface of 18 cm x 23 cm and was filled with a watery solution of benzoic acid and some drops of detergent to reduce surface tension. The traps were emptied once a week and all insects were transferred into 70% ethanol for storage. Since some trays were destroyed by wild boars, only 3 replicates per site and per week were included in the final analysis.

Bioassays

Females of each of the three species of pollen beetle parasitoids were tested in a two-choice olfactometer bioassay for odour preferences (**paper I**). I used a Y-shaped glass tube with 15 mm diameter, 4 cm long arms and a 2 cm long base (Fig. 4). Metal clamps were used to connect further glass chambers to the Y-tube: A release chamber (2 cm in length) was connected to the base of the Y-tube and its other end was connected to a flowmeter and a suction pump. Both arms of the Y-tube were connected to terminal chambers of the same length as the release chamber: The terminal chambers were either empty or contained the stimulus.

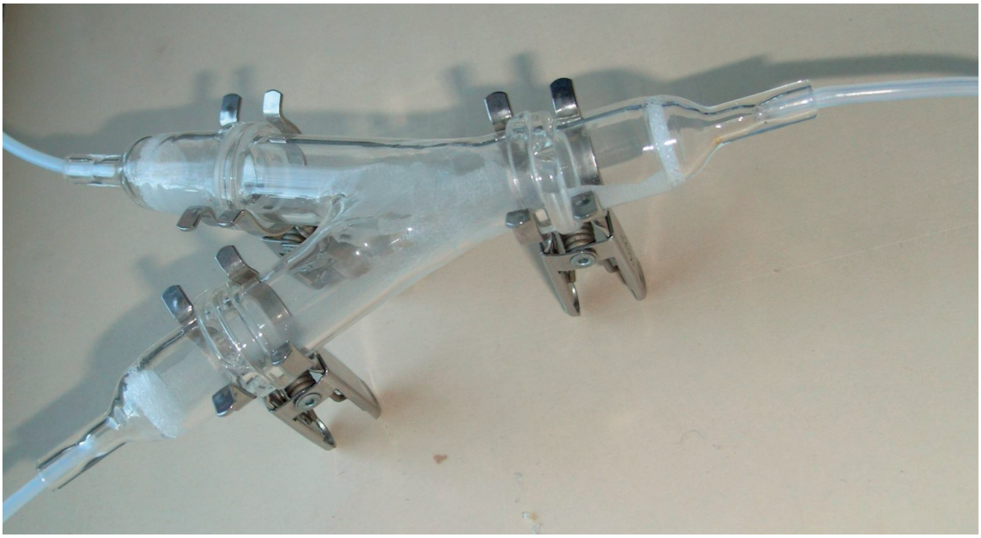

Figure 4:
Olfactometer used for the indoor bioassays in paper I. The release chamber is to the right, the two terminal chambers to the left of the Y-tube.

Locomotory active female parasitoids were removed from their container with an aspirator and transferred individually into empty Petri dishes. After acclimatisation, each parasitoid was covered by an upright standing release chamber and placed under a light source, until it began to walk into the release chamber. Once inside the release chamber, I connected the chamber to the rest of the Y-tube. A parasitoid that reached a terminal chamber within 5 minutes was counted as having made a decision. I provided the parasitoids with following stimuli:

a) Odours from different developmental stages of host larvae, versus an empty chamber.

b) Odours from developmental stages against each other.

c) Odours from the two smallest stages in combination with uninfested oilseed rape as background odour, versus background odour only.

d) Odours with empty chambers with traces (footprints, faeces) of host larvae, versus a clean empty chamber.

Insect identification

I have identified all insects using the most recent taxonomic literature, comparing with reference specimens at the Entomological Collection of the Biological Museum of Lund University, and consulting taxonomists at this and other museums for verification (see Acknowledgements).

Some groups of Hymenoptera had to be excluded due to the lack of reliable identification literature (e.g. male Cryptinae; see details in **paper IV**). Heteroptera were only included in **paper III**. For time reasons, I had also to exclude other potential host groups, such as Diptera, Homoptera, and all predatory arthropods (mainly spiders and beetles of the families Carabidae and Staphylinidae).

Statistical analysis

In **paper I**, the parasitoid preferences in the olfactory bioassays were tested with the G-test of goodness of fit against an expected 50:50 ratio (McDonald 2014).

In **paper II**, the relative effects of each potential landscape predictor on host or parasitoid abundances were evaluated in a multimodel inference approach with model averaging, which allows for uncertainty in choice among multiple competing models (Burnham & Anderson 2002). All statistical analyses were calculated in R version 3.3.3, using the packages 'MASS' (Ripley et al. 2017), 'car' (Fox et al. 2017) and 'MuMIn' (Bartoń 2016).

Paper III includes a multivariate analysis of the incidences (i.e. presences and absences) of parasitoids and their hosts. Only those species were included in this paper which can potentially interact with each other based on host-parasitoid records in the literature. All included species were analysed as multiple response variables; their response to landscape predictors was tested with distance-based redundancy analysis (dbRDA), an ordination technique which tests the proportion in the variance in species composition that can be predicted from a linear combination of predictor variables. All statistical analyses were calculated in PRIMER 6.0 (Clarke & Gorley 2006) with the PERMANOVA+ add-on (Anderson et al. 2008).

In the same paper, also two qualitative food web metrics were regressed on the landscape predictors. The food web metrics were calculated from bipartite host-parasitoid matrices using the 'bipartite' package in R (Dormann et al. 2008).

In **paper IV**, species abundance models were fitted to the empirical data with maximum likelihood tools in the R package 'sads' (Prado et al. 2018). Further R packages used for this paper were 'ape' (Paradis et al. 2004), 'BiodiversityR' (Kindt 2017), 'boot' (Canty & Ripley 2017), 'MuMIn' (Bartoń 2016), 'pgirmess' (Giradoux 2017), 'spdep' (Bivand et al. 2017), and 'stats' (R Core Team 2017). In order to disentangle the effects of environmental variation and of geographical distance on the parameters of species abundance distributions, I used a relatively simple regression approach: After accounting for environmental effects (which I attribute to niche assembly) on the response variable, the residuals of that regression were tested for spatial autocorrelation to identify effects of spatial distance (which I attribute to dispersal assembly).

Results and discussion

How sympatric parasitoids of the pollen beetle avoid competitive exclusion

My findings in **paper I** clearly demonstrate that there are temporal, spatial and behavioural differences between the three sympatric parasitoids of the pollen beetle, so that these species can be assumed to have differentiated their ecological niches in order to coexist while sharing the same host species. When the results of my indoor bioassays and phenological observations are seen in the context of the outdoor bioassays and behavioural observations of the second author, the following picture emerges: *Phradis interstitialis* turns out to be active early in the season (during the time when oilseed rape is in the green bud stage), to prefer odours of infested buds over noninfested, and to oviposit into buds which contained only pollen beetle eggs. *P. morionellus* turns out to be active later in the season, to prefer odours of infested buds and infested flowers over uninfested, and to oviposit into buds which contained only larvae. *Tersilochus heterocerus* is active during the entire season, prefers odours of infested flowers over uninfested, oviposits into larvae in open flowers, and is attracted to odours from first-instar pollen beetle larvae, both in the presence and in the absence of uninfested plant odour. Both *Phradis* species appear thus to be separated on a temporal scale and also by preference for different host stages, whereas the larval parasitoids *P. morionellus* and *T. heterocerus* are separated by choice of microhabitat for oviposition: *P. morionellus* oviposits into larvae in buds, and *T. heterocerus* into larvae in flowers.

These results also indicate that *T. heterocerus* parasitizes its host in a younger developmental stage than large second instar larvae, as has been suggested by previous authors (Nilsson 2003, Williams & Cook 2010): Our tested females avoided odours of large second instar larvae (3-5 mm), and preferred odours from small (young first instar, 1-1.5 mm) and intermediate-sized (older first instar, 2-2.5 mm) larvae. From this, I conclude that pollen beetle larvae probably get parasitized earlier than at the age when they are big enough to actively drop from the plant. Figure 5 shows a parasitized older first instar larva (2.3 mm in length) in the process of ecdysis into second instar.

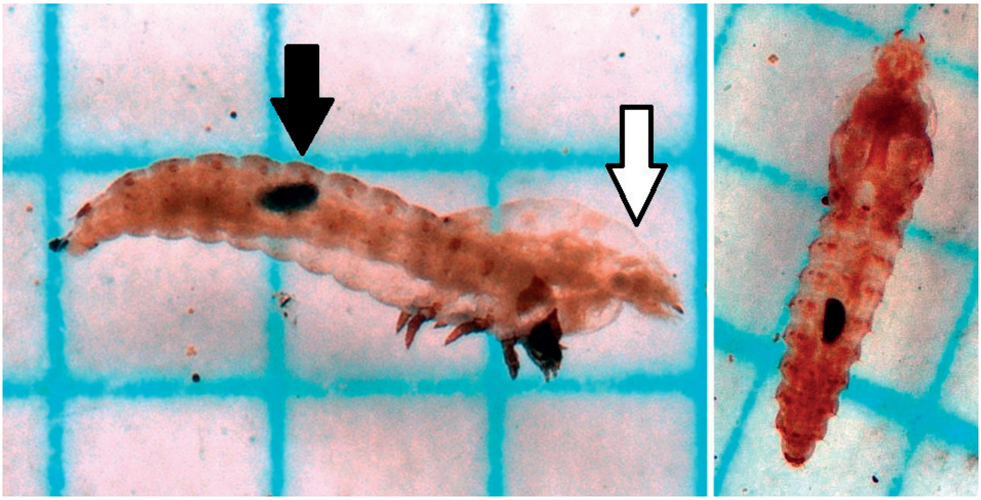

Figure 5:
Parasitized pollen beetle larva in the process of ecdysis from first instar into second instar, a) lateral, b) dorsal view. The black arrow points to the black egg, indicating parasitization by *Tersilochus heterocerus*, in the abdomen of the late first-instar larva; the white arrow points to the head of the emerging teneral second instar.

This study did not take into account larval competition among the three species of parasitoids. It was already noted by Osborne (1960) that *Tersilochus heterocerus* larvae often failed to complete their development when other parasitoid species were present in the same host, which indicates a competitive superiority by both *Phradis* species in cases of multiparasitism. Furthermore, he encountered "numerous examples" of adult pollen beetles who carried 1-3 encapsulated black egg shells in their fat bodies, which is evidence that the host's immune system is capable to effectively eliminate *T. heterocerus*. Still, parasitisation frequency of pollen beetle larvae by *T. heterocerus* (i.e. the percentage of collected pollen beetle larvae who contain black eggs) is the most commonly used response variable in oilseed rape biocontrol studies (Williams 2010) although the examples from Osborne (1960) indicate that parasitisation of pollen beetle larvae by *T. heterocerus* does not always lead to successful mortality of the host. In order to broaden our understanding of natural control, it might therefore be meaningful to quantitatively assess the actual effectivity of this parasitoid species to kill its host and to survive larval competition with both *Phradis* species. This might be achieved by collecting parasitised pollen beetle larvae for breeding experiments in order to quantify how many beetles and parasitoids will hatch successfully, and to determine whether the surviving beetles were parasitised only by *T. heterocerus* or by the *Phradis* species too. The identification of encapsulated parasitoid remainders in the adult beetles may be facilitated by molecular methods, since all three species are on GenBank.

The cabbage stem weevil uses the landscape on a smaller scale than its two ichneumonid parasitoids

My results in **paper II** do not support the theoretical expectation that parasitoids use the landscape on a smaller spatial scale than their hosts: The abundance of adult cabbage stem weevils was best explained by the proportion of oilseed rape in the surrounding landscape at the 1000 m scale, while all other variables had considerably lower explanatory power. In contrast, none of the tested spatial scales (between 250 m and 2000 m) nor scale-dependent landscape variables explained the abundances of its parasitoids *Tersilochus obscurator* and *Stibeutes curvispina*: Pesticide application and host abundance were the most important predictors of *T. obscurator* abundances. For *S. curvispina* abundances, the only important predictor was host abundance. An explanation for this observed pattern might be that both parasitoid species utilise the landscape on a higher functional scale than their host, which is in contrast to several theoretical and empirical studies which suggested the opposite (Tscharntke & Brandl 2004). As suggested by Kristensen et al. (2013), the low dispersal estimates for parasitoids reported in literature may be an artifact from the restricted scale range of those studies. Ecologists need also to consider that the "functional spatial scale", resulting from spatial regression techniques, may tell us something about the minimum dispersal capacity of its organism, but not how far the organism is actually able to disperse, since there is no need to disperse over large distances if all requirements on the environment (food, shelter, reproduction) are met within the immediate vicinity. In order to gain a more detailed knowledge about the dispersal patterns of any particular species (i.e. whether it is a stenotopic species, a cultural species, a strong disperser, or an ubiquist), excessive sampling of dispersing individuals within and outside one focus patch would be necessary (Duelli & Obrist 2003, Tscharntke et al. 2005b).

A second important observation from this study is that the cabbage stem weevil abundances were nearly unaffected by insecticide residues, whereas the abundances of *T. obscurator* were strongly affected. This is consistent with other authors who found reduced abundances of this parasitoid species after insecticide application (Ulber et al. 2010b) and avoidance behaviour in *T. obscurator* females when offered leaves with dried pesticide residues (Neumann 2010). Consequently, when considering future management strategies to reduce cabbage stem beetle abundance and promote its natural enemies, it seems to be more promising to manipulate the proportion of oilseed rape in the landscape rather than to employ insectides.

The abundance peak of *S. curvispina* was slightly delayed compared to *T. obscurator*, which is consistent with the hypothesis that *S. curvispina* is a prepupal/pupal parasitoid (Nissen 1997, Horstmann 2010); it does therefore not need to be in the field before the mature host larvae start dropping from the plant in order to pupate in the soil. In contrast, *T. obscurator* oviposits into host larvae through the plant tissue while these are still mining inside the stem or petioles (Ulber et al 2010a) and it needs therefore to arrive earlier. This temporal separation between the two species might also partially explain why *S. curvispina* was not affected by insecticide residues: *T. obscurator* arrives closer to the spraying date (which was in late April or early May) and it is also more exposed to physical contact with insecticide residues, as it has to actively walk on the plant while locating its host.

When considering pesticide effects on my abundance data, an obvious problem is that the farmers have not used the same pesticide treatment (5 of the sites were treated with pyrethroids, 1 site with neonicotinoids and 1 site with both), which makes it difficult to draw general conclusions. As pyrethroids and neonicotinoids are likely to have differential effects on parasitoids (Neumann 2010), more field studies are needed to evaluate this. The effect of neonicotinoids on parasitoid abundances will be addressed separately in another publication (Klatt et al., unpubl. data).

Landscape configuration affects the species composition of parasitoid and host communities and their interaction networks

On community level, the presences and absences of several parasitoid species and host species (**paper III**) were affected by several landscape variables: Distance from the collection site to forested land, together with oilseed rape within a 1 km radius, was an important predictor of variation in community composition of both parasitoid and host communities. It should be noted that this effect of landscape configuration applies only to those species which contributed to variation in community composition (i.e. not for those species that were present in every single site - pollen beetle, cabbage stem weevil, and some others - because their contribution to the variation in presences and absences is zero). Interestingly, the distance from the previous-year oilseed rape field did not affect the species composition in neither trophic level, indicating that it is irrelevant for the presence or absence of parasitoid species whether their hibernation site is 30 m or 1061 m away from the sampling site. Therefore, it seems likely that parasitoids can easily overcome this distance by their flight ability.

The host-parasitoid interaction networks in **paper III** became more asymmetric with increasing distance from forested area, due to relatively fewer pest than parasitoid species. This supports our expectation that the proximity of forests affects the number of host species positively, in contrast to weak effects on the number of parasitoid species. This can be explained by the fact that several host species hibernate under leaf litter; sites that are situated in larger distances from forests get colonized by less host species. As a practical implication of this study, it can be concluded that if farmers grow oilseed rape in regions that are situated far away from forests, then this is likely to minimize recolonization by pest species and at the same time it will attract more species of parasitoids from the open landscape.

Relative contribution of niche assembly and dispersal assembly to species abundance distributions

In **paper IV**, the bended powerlaw distribution (i.e. a powerlaw with an exponential cutoff function) turned out to best describe both the parasitoid and the beetle the metacommunity. The value of its slope parameter indicates that the metacommunity is not sufficiently explained by dispersal and demographic stochasticity, but that some additional constraints act on the species abundances.

On local community level, I found no effect of geographical distance on the slope parameter of the parasitoid species abundance distribution, but a significant contribution of the first principal component of environmental variables. Seen through the glasses of metacommunity theory, this result implies that parasitoids may be sufficiently mobile to track environmental variation between the local sites (up to 22.3 km distance). In contrast, I found no significant effect of environmental variables on the abundance distribution in local beetle communities; however, there was a significant spatial autocorrelation in the bending parameter of the beetle species abundance distribution. This bending parameter can be interpreted as model fit of the most common portion of the species abundance distribution (McGill 2011); consequently, the most common beetles in oilseed rape are stronger affected by geographical distances than the rarer beetle species. Spatial autocorrelation is often seen as a nuisance by ecologists, but it can also be seen as a source of information (de Knegt et al 2010): Here, it tells us that the commonness of beetles was most similar at geographical distances 4-6 km between the sites, which can be interpreted as dispersal limitation in the most abundant species. From the same results, it may also be concluded that the commonness of beetles in oilseed rape is stronger affected by geographical distance than the commonness of parasitoids.

I draw all my conclusions about niche assembly from a relatively simple regression of environmental variables on the parameters of a species abundance distribution, whereas my conclusions about dispersal assembly were drawn from the extent of spatial autocorrelation in model residuals. This methodological approach is perhaps too simplistic, as it ignores the potential problem that there may be even an intrinsic spatial component in the environmental effects. This problem can be adressed with more sophisticated statistics, e.g. multivariate variation partitioning which separates the variation in multivariate community data into four components: Environmental, spatial, an interaction of environmental and spatial, and remaining variance in the data (Méot et al. 1998, Dray et al. 2012, Legendre et al. 2012). However, there is some debate whether these variation partitioning methods are reliable due to several confounding factors (Tuomisto et al. 2012, Brown et al. 2017).

Residents and tourists in oilseed rape fields

In **paper IV**, I tested also the hypothesis that the abundance distribution of resident members of the oilseed rape habitat is structured by classical niche assembly mechanisms whereas occasional immigrants from outside the habitat are structured by stochasticity. However, this hypothesis was not supported by my empirical data, implying that demographic stochasticity and a high dispersal rate are sufficient to explain the patterns of commonness and rarity in oilseed rape residents, whereas the the abundance patterns of occasional immigrants likely depend on additional contraints - possibly alternative food sources in the surrounding landscape.

Although several families were excluded for pragmatic reasons, I have still identified 77 species of parasitoids and 65 species of beetles (paper IV: Tab.S2 and S3), of which 24 parasitoid species and 15 beetle species can be classified as "residents" (i.e. associated with oilseed rape through their known biology) and 53 parasitoid species and 50 beetle species can be classified as "tourists" (i.e. not having any known association with this habitat).

As expected from the niche-assembly perspective, those beetle species connected to high economic losses in oilseed rape (and some of their parasitoids) had the highest abundances; on the other hand, the species abundance distribution also revealed relatively high abundances in species which are normally not associated with oilseed rape: Namely, *Sitona lineata*, *Protapion fulvipes* and *Protapion trifolii* were among the 10 most abundant beetle species in the metacommunity, although they are normally associated with clover. This can only be explained by spillover from adjacent habitats in the same landscape.

Literature about oilseed rape is usually only concerned with species that are thought to have highest economic impact. For this reason, the diversity of insects in this monoculture, and particularly the diversity of parasitoids, is rarely studied: Usually, entomological publications about this ecosystem either concentrate on empirical data about very few species, namely those that are associated with the most severe agricultural pests (Nilsson & Andreasson 1987, Veromann et al. 2006, Šafář & Seidenglanz 2018) or the authors compile anecdotical evidence about all species recorded in this study system during the 20th century, several of which are taxonomically synonymous within the same tables (Alford et al. 2003, Ulber et al. 2010a). Inventories of parasitoids in oilseed rape where more than 11 species are identified to species level are, to my knowledge, virtually nonexistent in Palearctic literature. The only detailed one I am aware of is qualitative, i.e. it gives for each species only symbols indicating relative density categories instead of actual numbers (Nerad et al. 2011). There is some Nearctic quantitative data for selected taxonomic groups obtained by breeding from *Ceutorhynchus* beetles (Mason et al. 2011, 2014) or from the cabbage fly *Delia radicum* (Hemachandra et al. 2007). My work contributes thus to the field of oilseed rape literature with a wider community perspective which also takes into account spillover processes from other crops.

Interestingly, I have never found *Brachyserphus parvulus*, *Diospilus capito* nor *Euderus albitarsis* in any of the 26 Swedish winter OSR sites (sampled by water traps), but on the other hand I found these three species exclusively in 16 Swedish summer OSR sites, where they were sampled with a sweep net (Klatt et al., unpubl. data). It is possible that this reflects information about the temporal niche of these species, as summer OSR flowers later; on the other hand, this observation might also be affected by the different methodology.

Concluding remarks

From the phenological results in papers I and II, it can also be concluded that the parasitoids of the most common two beetle species in Swedish oilseed rape have slightly different temporal activity peaks. This information may be relevant for the timing of chemical pest control applications.

Taken together, my results from paper II, III and IV suggest that parasitoid wasps in the oilseed rape habitat can disperse over larger distances than what was previously thought. Hence, there is a need for a large-scale perspective on parasitoid abundances that reaches beyond a few kilometres. Also, I conclude that the most common beetle species in oilseed rape seem to have a stronger dependence on geographical proximity than the most common parasitoids. These theoretical considerations about differential dispersal capacity in common oilseed rape pests and their parasitoids may have implications for applied agricultural entomology, most notably for those who develop specific strategies for integrated pest management in oilseed rape fields in order to promote the persistence and the diversity of parasitoid wasps in the agricultural landscape.

Prospects for further research

Due to time limitations, I have not included additional landscape predictors which may also have potential influence on community composition (**paper III**) and abundance patterns (**papers III** and **IV**): Namely, additional non-crop habitats, such as hedgerows and field margin strips, may provide alternative hosts, refuge and energy sources for parasitoids (Tscharntke et al. 2005a, Duflot et al. 2015, Landis 2017). The same may be true with flowers in suburban and urban gardens, whose contribution to the maintenance of parasitoid diversity has long been underestimated (Galluzzi et al. 2010; but see Owen et al. 1981). In recent years, it was shown that horticultural area and floral resource additions increase parasitoid abundance and change their community composition (Bianchi et al. 2008, Egerer et al. 2018). The ecological impact of gardens deserves thus closer attention for the benefit of food production and biodiversity conservation in agricultural ecosystems (Goddard et al. 2010).

Natural communities are not only shaped by their recent environment, but also by their evolutionary history. An integration of community analysis and phylogenetic structure (Pillar & Duarte 2010, Peres-Neto et al. 2012) might help to explain the composition both of local communities and the metacommunity, since closely related species are more likely to have similar requirements than distantly related species. Phylogenetic constraints have rarely been taken into account in community analysis, but it is a promising new approach. For example, Bersier & Kehrli (2008) found a close relationship between food web structure and phylogeny. Since all empirical biodiversity samples are likely to carry some intrinsic phylogenetical information, it may be interesting to test how much of the variation in the data can be attributed to a shared evolutionary history of the involved species, before the effects of recent landscape parameters are taken into consideration.

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Populärvetenskaplig sammanfattning

VILKA EKOLOGISKA PROCESSER PÅVERKAR PARASITSTEKLAR OCH DERAS VÄRDAR I SKÅNSKA RAPSFÄLT?

Varje vår blommar rapsen i Skåne och man ser överallt rapsens gula färg i landskapet. I dessa gula fält myllrar det av insekter, och man förväntar sig kanske inte att hitta någon mångfald i en sådan monokultur. Men där finns inte enbart rapsbaggen, bondens stora fiende, utan även många andra arter: Några växtätande arter som äter olika delar av rapsväxten, många andra arter som är växtätarnas naturliga fiender, och ännu fler arter som är turister från det omgivande landskapet. I min avhandling undersökte jag dessa insekter och hur deras närvaro respektive antal kan förklaras med hjälp av ekologiska processer.

Hälften av alla kända flercelliga organismer på jorden är insekter. En stor del av jordens biologiska mångfald lever dessutom i sådana ekosystem som människan direkt kontrollerar, såsom jordbrukslandskapet. Jordbrukslandskapet har dock under de senaste decennierna förändrats för att möta den växande människopopulationens matbehov: Landskapet som tidigare varit karakteriserat av små fält och betesmarker med många obrukade ytor (skogsdungar, häckar, trädor, vall), har sedan 1960-talet förvandlats till ett alltmer homogen landskap genom större fält, minskning av obrukade ytor, plantering av genetiskt identiska monokulturer, och storskalig användning av bekämpningsmedel och konstgödsel. Forskningen visar att jordbrukets intensifiering leder till en nergång i den biologiska mångfalden och därmed även i de medföljande ekosystemtjänsterna, dvs. de ekologiska processer som direkt eller indirekt bidrar till människans välmående, som exempelvis pollinering, näringsämnescirkulation och biologisk skadedjursbekämpning genom skadedjurens naturliga fiender. Även om det är svårt att försöka beräkna ekosystemtjänstens värde i monetära termer, så har den sistnämnda tjänsten - enbart för USA - uppskattats till ca 4,5 milliarder dollar årligen. Därmed ligger det i människans intresse att forska om vad som påverkar skadedjurens naturliga fiender.

De studieorganismer som jag har valt i min avhandling är parasitsteklar, dvs. sådana steklar som lägger sina ägg i eller på andra insekters utvecklingsstadier. Stekellarven äter sedan upp värddjuret och dödar den. I skånska rapsfält hittade jag inte enbart sådana stekelarter som är förknippade med rapsbaggen och andra skadedjur, utan även många andra arter som man inte hade förväntat sig där. Det finns olika ekologiska teorier för att förklara mångfaldens variation mellan olika samhällen: Konkurrens mellan arterna, miljöfaktorer, slump och metasamhällsteorin. Det sistnämnda kan man förstå som en teori som knyter ihop flera lokala samhällen genom spridning av en eller flera av sina medlemmar: På detta sätt kan varje lokal samhälle ses som ett resultat av lokala processer (som miljöfaktorer och interaktioner) och processer som sker på en större skala (som spridningsmönster).

I min avhandling undersökte jag

- hur tre stekelarter undviker konkurrens trots att de delar samma värd - rapsbaggen (**uppsats 1**),
- vilka rumsliga skalor som är relevanta för den fyrtandade rapsviveln och två av dess parasitsteklar (**uppsats 2**), och
- hur landskapets sammansättning påverkar artsammansättningen och potentiella interaktioner hos parasitsteklar och deras värdar (**uppsats 3**), och
- hur miljövariation och geografisk distans påverkar arternas individantals-fördelning hos både parasitsteklar och skalbaggar (**uppsats 4**).

I de skånska rapsfälten angrips rapsbaggen av flera stekelarter. Om flera stekelarter går på samma värdart, kan man undra hur de kan existera på samma plats och med samma värd, dvs. utan att den ena arten konkurrerar ut den andra? I den första uppsatsen i avhandlingen undersökte jag därför hur tre nära besläktade rapsbaggeparasitsteklar klarar av att samexistera. Det visade sig att deras ekologiska nisch (specialisering) skiljer sig i flera hänseenden, både när det gäller aktivitetstiden, val av mikrohabitat, och värdens utvecklingsstadium: Arten *Phradis interstitialis* är aktiv tidigare, när rapsen fortfarande är i knoppstadiet, har en doftpreferens för knoppar som innehåller rapsbaggeägg, och lägger sina egna ägg i rapsbaggens ägg. Systerarten *Phradis interstitialis* är aktiv senare under säsongen, attraheras både av rapsbaggeinfesterade knoppar och blommor, och lägger sina ägg i sådana knoppar som innehåller rapsbaggelarver. Den tredje arten, *Tersilochus heterocerus*, är aktiv under hela säsongen, har en doftpreferens för infesterade blommor, lägger sina ägg i rapsbaggelarverna i blomman, och attraheras av doften från första larvstadiet. I denna första uppsats var det speciellt spännande att upptäcka att den sistnämnda arten inte var attraherad till dofter från rapsbaggens andra larvstadium. Tidigare litteratur hade nämligen föreslagit att det är just det andra larvstadiet som *T. heterocerus* angriper, men mina resultat tyder på att stekelarten föredrar att parasitera yngre larver. De tre rapsbaggeparasitoiderna har alltså olika aktivitetstider, olika doftpreferenser, och föredrar olika värdstadier.

Dessa resultat kan vara relevanta för att planera en effektiv rapsbaggebekämpning inom ramarna för integrerat växtskydd, t.ex. genom att ta hänsyn till parasitsteklarnas aktivitetstider när bönderna väljer tidpunkt för insekticidbekämpning mot rapsbaggen.

I avhandlingens andra uppsats undersökte jag om steklarna sprider sig kortare avstånd än sina värdarter. Det är nämligen så att ekologisk teori förväntar sig att parasitsteklar, på grund av sin ringa kroppsstorlek och extrema specialisering, borde vara mindre rörliga än sina värddjur; värddjuren förväntas däremot ha en större aktivitetsradie än steklarna, speciellt om storleksskillnaden är stor. Jag testade denna förutsägelse med hjälp av insamlade och räknade fyrtandade rapsvivlar och två av dess parasitsteklar, och testade rumsliga skalor mellan 250 m och 2000 m. Mina resultat stödjer dock inte förutsägelsen: Medan rapsproportionen på 1000 m-skalan var den relativt viktigaste variablen för att förklara rapsvivlarnas antal och alla övriga skalor och variabler hade mindre betydelse, så spelade ingen av de testade skalorna någon roll för parasitsteklarnas antal. Detta kan tolkas som att steklarna kan sprida sig över större distanser än de rumsliga skalor som jag testade.

Däremot påverkade värdantalet båda parasitstekelarterna, och en av dem - den fyrtandande rapsvivelns vanligaste parasitstekel, *Tersilochus obscurator* - påverkades dessutom signifikant av besprutning, medan själva rapsvivelns antal intressant nog inte påverkades alls. För att utveckla framtida integrerade rapsvivelbekämpningsstrategier, som också gynnar rapsvivelns naturliga fiender, verkar det därmed vara mera meningsfullt att manipulera rapsproportionen i landskapet än att spruta insektbekämpningsmedel.

I avhandlingens tredje uppsats undersökte jag hur artsammansättningen i flera parasitstekel- och värdsamhällen påverkas av landskapets sammansättning. Jag var speciellt nyfiken om variationen i artsammansättningen kan förklaras med a) avståndet mellan rapsfälten och insekternas övervintringsställen, och b) den totala ytan av raps inom 1 km radie. Här visade det sig att avståndet mellan rapsfält och närmaste skog, tillsammans med rapsytan, var en viktig förklaring till variationen i artsammansättningen för både parasitsteklar och värdar. Däremot spelade det ingen roll för parasitsteklarnas artsammansättning om avståndet från förra årets raps (där många av de involverade steklar förväntas att övervintra) var 30 m eller 1061 m. Därav drar jag slutsatsen att de involverade steklarna lätt kan övervinna detta avstånd genom sin flygkapacitet. Resultaten i andra uppsatsen visar även att skillnaden i artrikedomen mellan parasitsteklar och värdar blir större med avståndet från närmaste skog. Detta tolkar jag som att med växande avstånd till skog blir det relativt färre värdarter än stekelarter, förmodligen eftersom skogar fungerar som skalbaggekälla. Konsekvensen blir att det verkar vara en lämplig strategi att odla raps i sådana landskap som är långt bort från skogar, för att minska sannolikheten att rapsfälten blir koloniserade av skadedjursarter och samtidigt attrahera fler parasitstekelarter ur det öppna landskapet.

I avhandlingens fjärde uppsats undersökte jag hur konkurrens och spridning påverkar arternas antalfördelning hos både parasitsteklar och skalbaggar. Om antalet individer av varje art bestäms av arternas ekologiska nischer och därmed av konkurrensen mellan arterna om miljöns resurser, så förväntar man sig att variationen i arternas individantalsfördelning kommer att påverkas av miljövariationen. Om de involverade individantalen däremot bestäms av begränsad spridning, så förväntar man sig att antalvariationen påverkas av avståndet mellan insamlingsställen. Jag hittade ingen effekt av avstånd, men en signifikant effekt av miljövariabler på parasitsteklarnas antalsfördelning, vilket kan tolkas som att parasitsteklar är tillräckligt mobila för att kunna sprida sig mellan fälten (upp till 22,3 km) och hitta rätt miljöer. Däremot påverkade avståndet de vanligaste skalbaggarnas antalsfördelning, medan miljövariablerna inte hade någon effekt. Detta kan tolkas som att dessa skalbaggsarter har begränsad rörlighet. Avståndeffekten för de dominerande skalbaggearterna var som tydligast på en skala 4-6 km mellan fälten.

Dessutom testade jag hypotesen att "invånarna" (sådana arter i metasamhället som kan kopplas till rapsen genom sin biologi) borde ha en individantalsfördelning som bäst förklaras med klassiska nischbaserade modeller, medan "turisterna" (sådana arter som inte har någon känd koppling till rapsen) borde ha en individantalsfördelning som bäst förklaras av slumpmässiga modeller. Mina resultat tyder dock precis på det omvända: "Invånarnas" individantalsfördelning förklaras bäst med av modeller med slumpmässig befolkningsutveckling och hög spridningsförmåga, medan "turisternas" individantalsfördelning avviker såpass mycket från slumpen att den sannolikt styrs av ytterligare deterministiska faktorer. En möjlig förklaring är att rapsspecifika arter har alla sina ekologiska behov tillfredställda inom habitatet medan "turisternas" individantal styrs av ytterligare variabler såsom mat- och värdkällor i det omgivande landskapet, eftersom varje "turist" kan antas vara "invånare" någon annanstans.

Sammantaget visar mina resultat att parasitsteklar och skalbaggar i rapsfälten styrs både av konkurrens (som leder till nischdifferentiering) och av spridningsprocesser. Mina resultat tyder också på att parasitsteklar i allmänhet verkar ha en högre spridningsförmåga än man hittills trodde. Om vi alltså vill strukturera jordbrukslandskapet så att den gynnar skadedjurens naturliga fiender, så behövs ett större landskapsperspektiv än bara några kilometers omnejd kring fältet.

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I **Josef Berger**, Martin Jönsson, Katarina Hedlund & Peter Anderson (2015): Niche separation of pollen beetle parasitoids. *Frontiers in Ecology and Evolution* 3:45. doi: 10.3389/fevo.2015.00045

II **Josef Berger**, Helena Hanson, Peter Anderson, Katarina Hedlund: The role of landscape scale for the cabbage stem weevil and its parasitoids. (Manuscript)

III **Josef Berger**, Klaus Birkhofer, Helena Hanson, Katarina Hedlund (2018): Landscape configuration affects herbivore-parasitoid communities in oilseed rape. *Journal of Pest Science* 91: 1093-1105. doi: 10.1007/s10340-018-0965-1

IV **Josef Berger**, Katarina Hedlund, Peter Anderson, Olle Anderbrant: Effects of environmental factors and geographical distance on the patterns of rarity and commonness of insects in oilseed rape fields (Manuscript)

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