Pest prevention in *Brassica* vegetables:

relating ecosystem services and disservices to landscape

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Dipl.-Biol. Martin Ludwig

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Referent:	Prof. Dr. Hans-Michael Poehling
Korreferent:	Prof. Dr. Klaus Hövemeyer
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Abstract

Agricultural production is claimed to use integrated pest management strategies to reduce threads arising from chemical crop protection. Integrated pest management considers all available pest management techniques, thereby prefers environment friendly techniques and minimises chemical pesticide use. The joint project ‘WeGa’ aimed to develop integrated pest management strategies using vegetable *Brassicas* as model crop. This thesis contributes by characterising landscape effects (with special attention to oilseed rape witch is closely related to *Brassica* vegetables) on pest and natural enemy presence on Brussels sprout plants. The thesis further investigates how weather conditions and crop cover nets influence colonisation and infestation of Brussels sprout plants.

The first chapter tests effects of potential source habitats and weather conditions on colonisation of Brussels sprouts by different pests and their natural enemies. Colonisation by cabbage whiteflies increased with upwind oilseed rape area in up to 1 km from the study site, pointing towards passive downwind transport. Colonisation by cabbage aphids increased with downwind oilseed rape area in 1 km radius, implying that aphids can be attracted upwind for about 1 km. This is surprising, as aphids are known to be transported downwind. The number of syrphid larvae did not respond to landscape characteristics but was positively related to prey (mainly whitefly) abundance.

The second intensely investigates the importance of oilseed rape area for colonisation of Brussels sprouts by cabbage whiteflies, the most abundant pest species in our study chapter more. Upwind oilseed rape area in wide landscapes (2-8 km radius) explained colonisation remarkably better than oilseed rape area in local landscapes (0.2-1 km radius). This can be explained by flight behaviour of cabbage whiteflies, which ignore host cues at the beginning of migratory flights.

The third chapter evaluates the effect of crop cover nets on different pests and their natural enemies in Brussels sprout fields. Commonly used 0.8 mm nets reduced colonisation by cabbage whiteflies and spiders, but their effect decreased during the growing season.

The fourth chapter investigates to what extend results on factors driving colonisation in early summer, gained on standardised plants, can be transferred into crop production situation in Brussels sprout fields. The positive effect of oilseed rape area on the most abundant pest, cabbage whitefly, persisted throughout the cropping season. In contrast, further landscape effects on colonisation by different pest species disappeared, probably due to less standardised and population growth affected situation in Brussels sprout fields. This shows that landscape effects on colonisation can, but not necessarily have to, determine pest densities even shortly before harvest.

In conclusion whitefly pest pressure can be of high importance even if the local landscape is poor in oilseed rape as colonisation by whiteflies was most strongly affected by oilseed rape area in radii > 1 km. The cultivation of *Brassica* varieties sensitive to cabbage whitefly infestation in landscapes with high amount of oilseed rape area in the wide surroundings (> 1 km radius) implies a high need for crop protection by e.g. the use of crop cover nets. Following suggestions are made to increase crop protection efficacy: nets should be installed in time and kept close; natural enemies could be released under nets; nets might be used to reduce initial colonisation by pests and then be removed to allow pest control by natural enemies; promoting natural enemies such as syrphids and parasitoids, e.g. by flower strips, can be effective as syrphids are attracted by high densities of prey including whiteflies.

Key words: Brussels sprout, cabbage whitefly, oilseed rape

Zusammenfassung

Die Landwirtschaft ist gefordert mittels integriertem Pflanzenschutz Risiken durch Agrochemikalien zu reduzieren. Integrierter Pflanzenschutz berücksichtigt alle zur Verfügung stehenden Methoden und bevorzugt umweltfreundliche Verfahren, um den Einsatz chemischer Pflanzenschutzmittel zu reduzieren. Ziel des ‚WeGa'-Netzwerkes war die Entwicklung neuer Methoden des integrierten Pflanzenschutzes am Beispiel von Kohlgemüse. Diese Arbeit trägt dazu bei, indem sie die Effekte von Landschaftsbestandteilen (insbesondere die von mit Kohlgemüse verwandtem Raps) auf Schädlinge und Nützlinge von Rosenkohl beschreibt. Weiterhin werden Einflüsse von Wind, Temperatur und Pflanzenschutznetzen auf Besiedlung und Befall von Rosenkohlpflanzen untersucht.

Das erste Kapitel beleuchtet den Einfluss potentieller Quellhabitate und Wetterbedingungen auf die Besiedlung von Rosenkohl durch Schädlinge und Nützlinge. Die Besiedelung durch die Kohlmottenschildlaus nahm mit dem windaufwärts gelegenen Rapsanteil im 1 km Radius zu, was auf eine passive Windverbreitung hinweist. Die Besiedelung durch die mehlige Kohlblattlaus nahm hingegen mit der windabwärts gelegenen Rapsfläche im 1 km Radius zu, was auf windaufwärts gerichtete Flüge in zu ihren Wirtspflanzen hindeutet. Dies ist überraschend, da im Allgemeinen auch für Blattläuse passive Windverbreitung angenommen wird. Die Zahl der Schwebfliegenlarven wurde nicht von den untersuchten Landschaftsbestandteilen beeinflusst, war aber durch die Zahl der Beuteorganismen, hauptsächlich der Kohlmottenschildlaus, positiv beeinflusst.

Im zweiten Kapitel wird die Bedeutung von Raps für die Besiedlung von Rosenkohl durch die Kohlmottenschildlaus, den häufigsten Schädling unserer Studie, genauer untersucht. Der windaufwärts gelegene Rapsanteil der großräumigen Landschaft (2-8 km Radius) erklärte die Besiedlung deutlich besser als der Rapsanteil in der lokalen Umgebung (0.2-1 km Radius). Dies kann dadurch erklärt werden, dass die Kohlmottenschildlaus zu Beginn ihrer Ausbreitungsflüge Wirtssignale ignoriert.

Das dritte Kapitel befasst sich mit der Wirkung von Pflanzenschutznetzen auf Schädlinge und Nützlinge in Rosenkohlfeldern. Im Gartenbau verbreitete Netze mit einer Maschenweite von 0,8 mm reduzierten die Besiedlung durch die Kohlmottenschildlaus und Spinnen, wobei diese Effekte im Laufe des Jahres schwanden.

Das vierte Kapitel untersucht, inwieweit sich die Ergebnisse zum Einfluss von Landschaftsbestandteilen auf die Besiedlung standardisierter Pflanzen im Frühsommer auf die Situation im Rosenkohlabbau übertragen lassen. Der positive Effekt von Raps auf den häufigsten Schädling, die Kohlmottenschildlaus, war im Rosenkohlanbau während der gesamten Anbauperiode zu finden. Im Gegensatz dazu ließen sich weitere Landschaftseffekte auf die Besiedlung durch verschiedene Schädlingsarten hier nicht nachweisen, was vermutlich auf die weniger standardisierte und durch Populationswachstum beeinflusste Situation in Rosenkohlfeldern zurückzuführen ist. Dies zeigt, dass Landschaftseffekte auf die Besiedlung den Schädlingsbefall bis zum Erntezeitpunkt bestimmen können, aber nicht müssen.

Es wird gefolgert, dass bezüglich bestimmter Schädlinge (hier Kohlmottenschildlaus) auch dann mit hohem Schädlingsdruck gerechnet werden muss, wenn die nahe Umgebung nur eine geringen Rapsfläche aufweist. Die Ursache ist, dass für die Besiedlung hauptsächlich Rapsflächen in der weiteren Umgebung (> 1 km Radius) relevant sind. In Landschaften mit hohem Rapsanteil in der weiteren Umgebung muss beim Anbau von Kohlsorten, die für den Befall durch die Kohlmottenschildlaus anfällig sind, mit einem hohen Pflanzenschutzbedarf gerechnet werden. Die Wirksamkeit von im biologischen und integrierten Pflanzenschutz relevanten Maßnahmen könnte wie folgt gesteigert werden: Pflanzenschutznetze sollten rechtzeitig ausgebracht und möglichst undurchlässig gehalten werden; Ausbringung von Nützlingen unter den Netzen; Netze könnten zum Herabsetzen der Anfangsbesiedlung durch Schädlinge genutzt und dann entfernt werden um Schädlingskontrolle durch natürliche Gegenspieler zuzulassen; natürliche Gegenspieler wie Schwebfliegen und Parasitoide können z.B. durch Blühstreifen gefördert werden um Schädlinge zu reduzieren, Schwebfliegenlarven zeigten hierfür Potential, da ihre Dichte mit der Dichte der Beuteorganismen, auch der Kohlmottenschildlaus, zunahm.

Schlagwörter: Rosenkohl, Kohlmottenschildlaus, Raps

General introduction

Ensuring the production of food for a growing world population is one of the major tasks of our time (Godfray *et al.*, 2010). Crop pests and pathogens can cause remarkable yield loss and therefore a need for crop protection (Oerke & Dehne, 2004; BMEL, 2013). On the other hand, widespread traditional chemical crop protection causes threads to the environment (Carson, 1962; Lexmond *et al.*, 2015; Sluijs *et al.*, 2015) and humans (Carson 1962, Clarke et al. 1997, Blair et al. 2014). Therefore the European Union passed the 'Directive 2009/128/EG of the European Parliament and of the Council' to reduce risk and impacts of pesticide use on human health and the environment. Germany implemented this directive into national law with the 'national action plan on sustainable use of plant protection products' (Nationaler Aktionsplan zur nachhaltigen Anwendung von Pflanzenschutzmitteln; BMEL, 2013). In this plan the federal ministry of food and agriculture aims to reduce risks to the environment that emerge from the use of plant protection products by 30 % until 2023. This aim shall be reached by advancements of integrated pest management (BMEL, 2013). The 'Food and Agriculture organisation of the United Nations' defines integrated pest management (IPM) as " […] careful consideration of all available pest control techniques and subsequent integration of appropriate measures that discourage the development of pest populations and keep pesticides and other interventions to levels that are economically justified and reduce or minimize risks to human health and the environment. IPM emphasizes the growth of a healthy crop with the least possible disruption to agro-ecosystems and encourages natural pest control mechanisms." (FAO, 2016).

This thesis was part of the joint project 'reliability through sustainable crop protection' (Sicherheit durch nachhaltigen Pflanzenschutz) within the 'competence network: value chain horticulture' (Kompetenznetz: Wertschöpfungskette Gartenbau [WeGa]). The joint project aimed to foster a paradigm shift from a curative, short term effective crop protection concept to a holistic crop protection concept with strong use of biotic interactions affecting the infestation dynamics of crop pests as required for integrated pest management (Smith *et al.*, 1976). The holistic crop protection concept in WeGa was based on three pillars: prediction, prevention and intervention. The predictive pillar incorporates the consideration of spatial composition and configuration of the landscape around a study site, weather conditions or (automated) pest monitoring to predict potential pest pressure and pest outbreaks. It aimed to define where and when preventive or interventive protection measures against a certain pest are needed. The preventive pillar aimed to keep herbivores under damage threshold by measures such as the support of natural enemies, site selection, planting and harvesting time and mechanical barriers (e.g. nets). The pillar of intervention was thought to control pests when preventive measures are not sufficient and to develop and use more environment friendly techniques compared to classical crop protection. It included measures such as the release of beneficial organisms, confusion as well as push and pull strategies.

Ecosystem services are defined as the benefits provided by ecosystems (MA, 2005). They can be divided into provisioning services, regulating services (e.g. pest control) and cultural services (MA, 2005). Negative ecosystem services, which reduce productivity and increase production costs, are called ecosystem disservices (Zhang *et al.*, 2007). The approach of integrated crop protection aims to encounter ecosystem disservices, such as pest damage, with the support of ecosystem services, such as pest control. Ecosystem services and disservices of concern for this thesis (pest control and pest damage) are provided by the landscape surrounding a crop field. Natural habitats as well as other crops play a role as additional food source, as refuge and as a source of spill-over (Blitzer *et al.*, 2012).

The development of holistic plant protection concepts needs to be based on solid knowledge on the ecology and behaviour of pests and natural enemies. Particularly knowledge on the importance of habitats which affect pests and/or natural enemies can be used to suppress pests and support natural enemies (Wissinger, 1997; Blitzer *et al.*, 2012; Dale *et al.*, 2013). This thesis focused on effects of different habitats in the landscape surrounding Brussels sprout fields on the abundance of pests and their natural enemies. It investigates colonisation processes at different spatial scales as well as crop infestation throughout the copping season, considers climatic conditions (prevailing wind directions and temperature) and evaluates broadly used preventive plant protection measures (crop cover nets).

Pests and their natural enemies on Brussels sprouts (*Brassica oleracea* var. *gemmifera*) were used as study system. Brussels sprouts originates from the wild cabbage (*B. oleracea* var. *oleracea)* from which also several other important vegetable crops stem from (cauliflower [*B. oleracea* var. *botrytis*], broccoli [*B. oleracea* var. *italica*], kale [*B. oleracea* var. *sabellica*], kohlrabi [*B. oleracea* var. *gongylodes*], red cabbage [*B. oleracea* var. *capitata* f. *rubra*], savoy cabbage [*B. oleracea* var. *capitata* f. *sabauda*], white cabbage [*B. oleracea* var. *capitata* f. *alba*] and others). Additionally Ethiopian mustard (*B. carinata* = *B. oleracea* x *B. rapa*) and oilseed rape (*B. napus* = *B. oleracea* x *B. rapa*) originate from the species (Ahuja et al. 2010). The family of Brassicaceae includes further crops such as mustard (*Sinapis sp.*) and radish (*Raphanus sp.*) and widespread weeds such as wild mustard (*Sinapis arvensis*), field pennycress (*Thlaspi arvense*) and shepherd's purse (*Capsella bursa-pastoris*). Several of the named crops are of global importance. In central Europe especially the growing of oilseed rape increased during the last decades (Statistisches Bundesamt, 2016).

The crops and weeds of the Brassicaceae family share several more or less specialised pests due to their close relationship and similar defensive compounds (mainly glucosinolates). This thesis was focused on pests and their natural enemies which can be found on leaves, such as cabbage whitefly (*Aleyrodes proletella*), cabbage aphid (*Brevicoryne brassicae*), peach-potato aphid (*Myzus persicae*), diamondback moth (*Plutella xylostella*), syrphid larvae, spiders and aphid parasitoids.

In chapter 1 we investigated the colonisation of young standardised Brussels sprout plants by different pests and their natural enemies. Thereby, we examined effects of different land use categories under consideration of weather conditions, i.e. temperature and wind direction. In this chapter we tested three hypotheses stating that:

1. oilseed rape, as the most widespread agricultural *Brassica* crop, is an important source habitat for *Brassica* pests and their natural enemies, while also other annual crops and permanent habitats can play a role,
2. thereby source habitats differ in importance according to their location relative to the study site and prevailing wind directions due to passive wind dispersal or olfactory orientation in host location and
3. dispersal activity and consequently colonisation increases with increasing temperature.

Chapter 2 focused on the effect of oilseed rape area on colonisation by the most abundant pest, cabbage whitefly. Thereby we used satellite data to examine colonisation from source habitats in distances of up to 8 km. In this chapter we tested three hypotheses stating that:

1. oilseed rape area on two different spatial scales affects colonisation of Brussels sprouts due to the existence of two whitefly morphs with different flight behaviour.
2. downwind transport is of importance for wide landscape-scale dispersal. Thus, giving additional weight to upwind located source habitats at the wide landscape-scale should increase the model's explanatory power.
3. upwind olfactory oriented flights play a role in host finding on the local scale. Consequently, giving additional weight to downwind located source habitats at the local landscape scale should increase the model's explanatory power.

All farms used crop cover nets to protect their *Brassica* vegetables from pests. Therefore, effects of crop cover nets on population development of different pests and their natural enemies were investigated in chapter 3. By considering findings of the first chapter we tested the importance of oilseed rape as source habitat for *Brassica* pests with a new dataset. In this chapter we tested three hypotheses stating that:

1. the abundance of pests and natural enemies on Brussels sprouts decreases with decreasing net mesh size.
2. the effect of nets reducing pest and natural enemy numbers decreases during the growing season.
3. infestation by pests predominantly specialised to the family Brassicaceae (i.e. cabbage whitefly, cabbage aphid and diamondback moth) increases with increasing amount of oilseed rape in the surroundings of Brussels sprout fields.

Colonisation intensity lays the foundation for future pest populations in crop fields. However, not colonisation itself but a potentially following high pest infestation is the direct cause of crop damage. Chapter 4 investigates to what extend results of chapter 1 on factors that drive colonisation of monitoring plants by pests and their natural enemies can be transferred into crop production situation in Brussels sprout fields during the course of the cropping season. We thereby considered infestation data from three consecutive years and aimed to answer the following questions:

1. Are the abundances of different pest and natural enemy species affected by the area of different land use types in the surrounding landscape?
2. Are the detected landscape effects strengthened by giving additional weight to upwind or downwind located habitats?
3. Do the detected landscape effects change throughout the growing season?

Chapter 1

Wind modulated landscape effects on colonisation of Brussels sprouts by insect pests and their syrphid antagonists

Martin Ludwig, Hella Schlinkert & Rainer Meyhöfer

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Abstract

Most crop fields are annually cleared including arthropod populations. Recolonisation depends on source habitat presence in the landscape and is often affected by weather conditions. This study identified source habitats and effects of temperature and prevailing wind direction on colonisation of Brussels sprouts by pests and their natural enemies. We sampled arthropods on standardised monitoring plants in 18 landscapes with different area of potential source habitats. Most abundant pests and antagonists were *Aleyrodes proletella*, *Brevicoryne brassicae, Plutella xylostella* and syrphid larvae. Variation in *A. proletella* colonisation was explained best by upwind area of oilseed rape (positive effect) and temperature (negative effect). Variation in *B. brassicae* colonisation was explained best by downwind area of oilseed rape (positive effect), whereas *P. xylostella* colonisation was marginally positively affected by downwind permanent habitats. Syrphid colonisation was significantly affected by prey abundance only (positive effect). Results suggest that *A. proletella* was transported downwind, whereas *B. brassicae* and *P. xylostella* locate host plants during an upwind flight for about 1 km. This is remarkable for aphids with often limited upwind flight ability. Considering prevailing wind directions improves forecasting the colonisation intensity by pests from important source habitats.

1. Introduction

The occurrence of insects on field crops, their population densities and population dynamics are affected by processes that occur at spatial scales larger than the field scale (Tscharntke & Brandl, 2004). In particular, regularly disturbed crop fields are colonised annually from surrounding landscapes (Wissinger, 1997; Blitzer *et al.*, 2012). Thus, integrated farming practices must consider the landscape scale if reliable colonisation forecasting is to be realised (Vialatte *et al.*, 2007). Colonisation (immigration), in addition to emigration, mortality and birth rates, determines pest presence and crop damage (Naranjo *et al.*, 2010). Emigration peaks from surrounding habitats can cause colonisation peaks in crops. Several insect groups show periodic migratory behaviour; for example, many aphid species switch hosts in spring and autumn (Döring, 2014). Polyvoltine insects usually stay in their habitats in summer as long as habitat quality remains suitable. Especially in agricultural landscapes, numerous habitats such as cereal or oilseed rape fields become unsuitable for herbivorous insects when the crops mature in summer (Wissinger, 1997).

Winter oilseed rape (*Brassica napus*) fields can be important source habitats for colonisation of *Brassica* vegetables (cultivars of *Brassica oleracea*) planted in early summer (Richter & Hirthe, 2014b; Ludwig & Meyhöfer, 2016). Both plants have a similar pest and natural enemy complex (Alford *et al.*, 2003). The area of winter oilseed rape has increased remarkably in the last few decades in Germany and now covers 11 % of total arable area (Statistisches Bundesamt, 2016). In particular, large numbers of *A. proletella* and *B. brassicae* overwinter on winter oilseed rape (Hafez, 1961; Collier & Finch, 2007). On the other hand, permanent habitats, such as forests, forest edges, grasslands and settlement areas, are often source habitats for pests and natural enemies in crop fields (Blitzer *et al.*, 2012). Moreover the abundance of syrphids with aphidophagous larvae increases with increasing presence of crop fields that serve as larval habitat (Meyer *et al.*, 2009) and overwintering sites (Raymond *et al.*, 2014). Crop fields, even without crops of the family Brassicaceae, may support *Brassica* pests by offering host plants among common weeds, e.g. *Thlaspi arvense* or *Sinapis arvensis* (Capinera, 2001).

Insect dispersal is affected by weather conditions (Khaliq *et al.*, 2014). Take-off behaviour usually has a minimum temperature threshold and the number of take-offs increases with temperature (Kring, 1972). Wind may affect dispersal in different ways. On the one hand, wind transports odours downwind. Consequently, insects can follow olfactory cues upwind to find food or mating partners (Moser *et al.*, 2009; Webster, 2012). This mainly applies to large insects, as flight ability increases with body size (Compton, 2002), whereas smaller insects can fly upwind into low wind speeds only. Dispersing small insects, such as aphids or whiteflies, are phototactically attracted to heights where they are passively transported by the wind (Döring, 2014), allowing them to move much larger distances than by active flight (Compton, 2002). Thus, source habitats located upwind from a focal habitat may have a larger effect on colonisation by small wind-dispersed insects than downwind located habitats (Fig. 1.1). Although it is known that colonisation processes can be affected by the wind, only few studies have investigated landscape effects combined with prevailing wind directions (Moser *et al.*, 2009).

This study aimed to identify source habitats in agricultural landscapes that affect colonisation of *Brassica* vegetables by important pest species and their natural enemies. It also investigated the weather conditions that can influence colonisation. We hypothesised that (1) oilseed rape, as the most widespread agricultural *Brassica* crop, is an important source habitat for *Brassica* pests and their natural enemies, while also other annual crops and permanent habitats can play a role, (2) thereby source habitats differ in importance according to their location relative to the study site and prevailing wind directions due to passive wind dispersal or olfactory orientation in host location and (3) dispersal activity and consequently colonisation increases with increasing temperature.

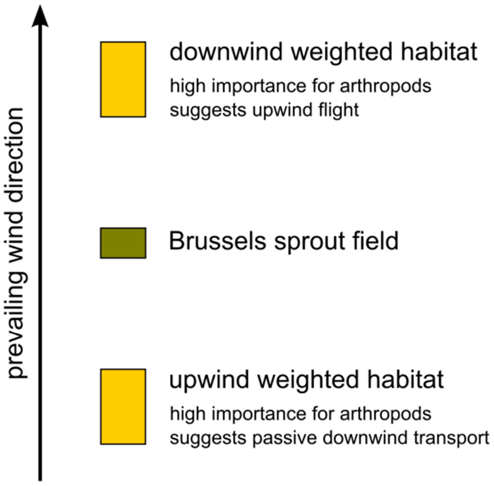

Fig. 1.1 Schema illustrating the high importance of upwind source habitats for passively downwind dispersed arthropods and the high importance of downwind source habitats for arthropods with (olfactory oriented) upwind flight.

2. Materials and methods

2.1. Field survey

Fields of Brussels sprouts on 18 organic horticultural farms located in southern Lower Saxony and northern North Rhine-Westphalia, Germany, were selected as study sites (Appendix A Fig. A.1). A wide variety of vegetables was grown on selected farms, including Brussels sprouts (planted between late April and early June) and other *Brassica* vegetables. All farms used nets to protect the *Brassica* vegetables from (large) insect and vertebrate pests. The nets had a mesh size of 0.8 or 1.3 mm or, on one farm, 7 mm. Insecticides were applied only after data were collected in July (described below). To quantify the area and location of potential source habitats, we recorded agricultural land use in circular 1 km radius areas around the study sites. Data regarding area and location of forests and settlements were taken from the official topographic-cartographic information system (ATKIS). Landscapes surrounding the study sites differed in land use and represented a gradient in area of agricultural land, permanent habitats and oilseed rape fields (Fig. 1.2). Weather stations (PCE-FWS 20; PCE Deutschland GmbH, Meschede, Germany) recorded wind direction and temperature at 15 minutes intervals at each study site.

Twenty monitoring plants on each study site were exposed monthly from May to October 2012 to record colonisation by pests. The monitoring plants were potted organic Brussels sprout plants, standardised in terms of exposure duration (2 weeks), soil type (mixture of 1.7 g water storing granulate [Broadleaf P4; AgriPol, Bournmoor, England] per litre potting soil), age (3 – 4 weeks) and variety (*Brassica oleracea* var. *gemmifera,* cultivar 'Topline F1'; Gartenbau Homann, Blender, Germany). We exposed 20 monitoring plants in two groups of 10 plants per study site. The plants were selected randomly from the stock. These two groups of monitoring plants were placed adjacent to the farmers' Brussels sprout fields (in 0.5 - 5 m distance), preferably on opposite sides of a field to account for spatial heterogeneity at the field scale. Water reservoirs were embedded in the ground to supply the plants with water via a wick.

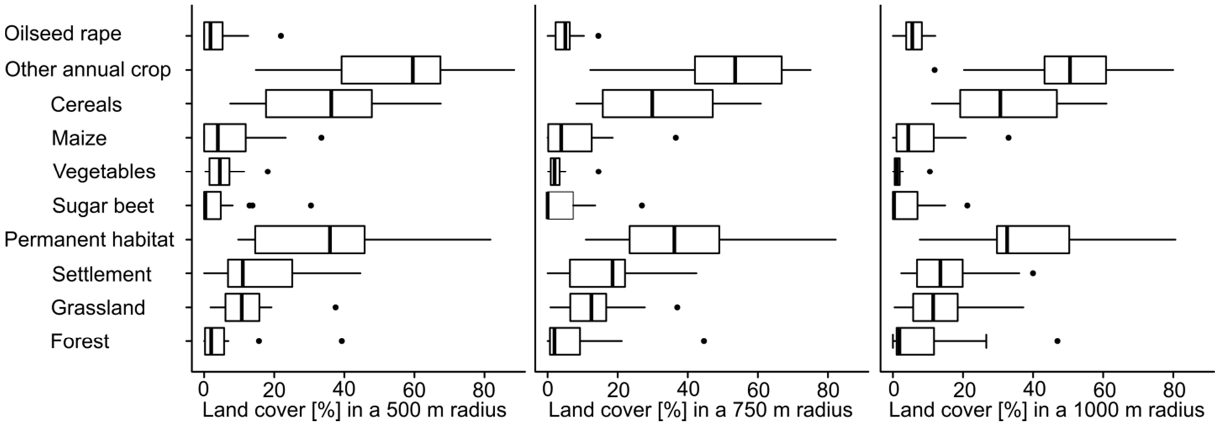

Fig. 1.2 Percentage land cover of analysed land use types (oilseed rape fields, other annual crop fields, permanent habitats) in circles of 500, 750 and 1,000 m radius around the 15 study sites. Percentage land cover is also shown for subcategories of 'other annual crop' and 'permanent habitats'.

Pests and natural enemies were counted on the monitoring plants after a two-week exposure. Terminal buds were opened to assess aphids, small caterpillars or syrphid larvae, which often hide there. Caterpillars that could not be identified in the field were collected and reared until identification was possible. Sampling was done monthly in six replications over time: 'June' (29.05.-13.06.2012), 'July' (27.06.-12.07.2012), 'August' (02.-13.08.2012), 'September' (31.08.-30.09.2012), 'October' (01.-12.10.2012) and 'November' (02.-13.11.2012).

We further monitored pest infestation in oilseed rape fields, which were presumably the main source habitat for Brussels sprout pest insects. One field close to each study site was selected to sample insects on stems and leaves of 20 oilseed rape plants close to the field edge. Plants were selected at random distances of 1 – 5 m. Oilseed rape plants had lost most of their leaves on several fields in July. Hence, in those fields, we sampled as many plants with remaining leaves as available, up to a maximum of 20 plants.

2.2. Data analysis

2.2.1. Generals

Three of 18 study sites were excluded from the analysis due to missing or outlying environmental data (see Appendix A.2 for details). To examine the effect of landscape, wind direction and temperature on Brussels sprout pest colonisation, we analysed the data collected in (early) July. Almost no colonisation of monitoring plants occurred in June, whereas July had the highest median colonisation of monitoring plants by *A. proletella*, *B. brassicae* and syrphids and the second highest colonisation by *P. xylostella* (Fig. 1.4). The colonising pests in July must have originated mainly from the surrounding landscape, as no older whitefly larvae, syrphid pupae and only a few aphids and diamondback moth pupae were detected in nearby Brussels sprout fields until July.

2.2.2. Colonisation of monitoring plants

One value for colonisation of monitoring plants was calculated for different insect species or groups at each study site. The mean number of *A. proletella* egg clutches per leaf was calculated including larvae that hatched during exposure time (4.678 larvae are equivalent to one clutch, see Appendix A Fig. A.3); mean numbers of *B. brassicae* aphids and *P. xylostella* caterpillars were calculated; and the numbers of syrphid eggs and larvae (no pupae were found in July) found per leaf at each study site were calculated. Syrphids, particularly *Episyrphus balteatus* as the dominant species in agricultural landscapes, do not lay eggs in the absence of prey (Verheggen *et al.*, 2008). Therefore, we included only plants that harboured prey (aphids or whiteflies).

2.2.3. Land use and weather conditions

Three categories of potential source habitats were defined: oilseed rape fields, other annual crop fields (mainly cereals, maize, vegetables and sugar beets) and permanent habitats (settlement area, grasslands and forests). We calculated the percentage area of these potential source habitats in circular landscape areas with radii of 500, 750 and 1,000 m around the study sites. To weight habitats according to their location relative to the study site and prevailing wind directions, the circular landscape areas were separated into eight sectors dedicated to wind directions (N, NE, E, SE, S, SW, W, NW; see Fig. 1.3). To account for higher importance of upwind source habitats for passively wind dispersed insects, the area of the three habitat categories was weighted. For this purpose, we first calculated the proportion of wind records (> 0.3 m/s) blowing from each of the eight sectors towards the study site during the time the monitoring plants were exposed. Second, the percentage area covered by the three habitat categories per sector was multiplied by the proportion of wind records blowing towards the study site. The sum of the resulting eight values (one value per sector) led to an area index with increased weight for upwind located habitats, hereafter called 'upwind weighted' area. To account for a higher importance of downwind source habitats for insects attracted by wind transported odours, we weighted the areas of the three habitat categories as follows: the percentage area covered by the three habitat categories per sector was multiplied by the proportion of wind records blowing from the study site towards the sector. The sum of these resulting eight values (one value per sector) led to an area index with increased weight for downwind located habitats, hereafter called 'downwind weighted' area.

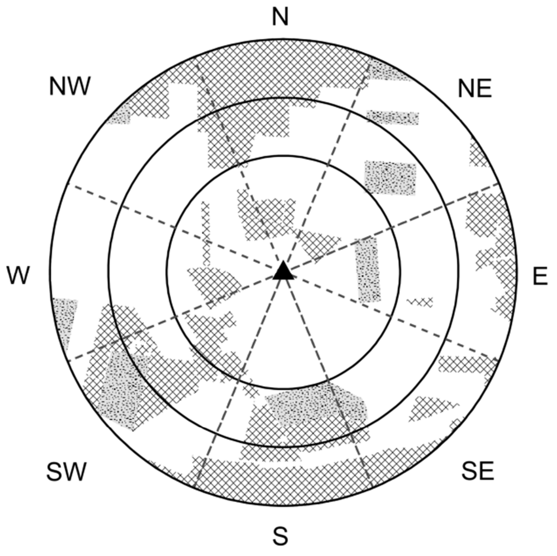

Fig. 1.3 Example of the division of the landscapes surrounding study sites (triangle) into circular areas of 500, 750 and 1,000 m radii (black circles) and into sectors dedicated to wind directions (dashed lines). The specific sectors' habitat area was multiplied by the percentage of wind events either in direction to the study site or in direction from the study site to weight land use type area by wind (oilseed rape: grey dotted, other annuals crops: white, permanent habitats: crosshatched).

Degree-days were calculated as a measure of temperature at each study site (Raworth, 1994), considering the species-specific threshold temperature for dispersal activity, i.e. 10 °C for *A. proletella* (Stein, 1958), 15 °C for *B. brassicae* and syrphids (Lowe, 1961; Gilbert, 1985) and 7 °C for *P. xylostella* (Goodwin & Danthanarayana, 1984). Only the time during the day with dispersal activity of the relevant insects was used when calculating the weather condition variables (degree-days and weighting of potential source habitats by wind direction). We used the time from 1 h after sunrise to 1 h before sunset for diurnal species (*A. proletella*, *B. brassicae* and syrphids) (Broadbent, 1949; Stein, 1958) and the time from 1 h after sunset to 1 h before sunrise for nocturnal *P. xylostella* (Goodwin & Danthanarayana, 1984).

2.2.4. Statistics

Regression models were used to analyse the effects of different land use types in the surrounding landscape and weather conditions on Brussels sprout colonisers. Response variables (numbers of *A. proletella* egg clutches, *B. brassicae*, *P. xylostella* caterpillars and immature syrphids on monitoring plants) were log-transformed to account for the non-normally distributed count data. First, we used the amount of one of the potential source habitats (oilseed rape fields, other annual crop fields or permanent habitats) in one of the spatial scales (radii of 500, 750 or 1,000 m) as a single explanatory variable for each response variable. Second, this basic set of models (nine models for each response variable) was modified using the area of potential source habitats with either upwind or downwind weighting of habitats (18 additional models for each response variable) and third by adding degree-days as an additional explanatory variable to the 27 named models (overall, 54 models per response variable). For syrphids additional 54 models were calculated that contained the mean abundance of potential syrphid prey per plant for each study site (sum of aphids, *A. proletella* egg clutches, larvae and adults) as additional covariable. Correlated explanatory variables ($R > 0.25$) were not used in the same model (Appendix A Table A.4). We ranked the models using the Akaike Information Criterion corrected for small sample size (AICc), which is a measure to assess relative model accuracy. The model with the lowest AICc (AICc_{min}) thereby represents the model with the highest accuracy, whereas all models within a $\text{AICc}_{\text{min}} + 2$ range ($\Delta\text{AICc} \leq 2$) are assumed to be of similar accuracy and are reported (Burnham & Anderson, 2002). Only effects with $p < 0.1$ in those models are discussed.

Analyses were performed using R version 3.3.0 (R Core Team, 2016). We used the package AICcmodavg version 2.0-4 to acquire AICc values (Mazerolle, 2016).

3. Results

3.1. Colonisation of monitoring plants

During the sampling period from June to November 2012, we recorded three species of phloem-sucking pests on the monitoring plants (a total of 1,739 plants corresponding to 12,225 leaves). *A. proletella* (77,435 egg clutches, 149,089 larvae and 82,882 adults) was the most abundant species followed by *B. brassicae* (29,977 individuals) and *Myzus persicae* (1,504 individuals). Additionally, caterpillars from seven Lepidoptera species were recorded. Among them *P. xylostella* (177 individuals) was the dominant species followed by *Pieris rapae* (64), *Pieris brassicae* (16), *Autographa gamma* (6), *Mamestra brassicae* (5), *Pieris napi* (2) and *Evergestis forficalis* (1). Syrphids were the most frequently observed group of predatory arthropods (355 eggs and 326 larvae), followed by spiders (125), common lacewings (59 eggs, 4 larvae) and coccinellids (4 larvae and 11 adults). The most important and abundant groups, namely *A. proletella*, *B. brassicae*, *P. xylostella* and syrphids, were considered in detail.

Dispersal activity throughout the season varied considerably. The monitoring plants were colonised by the main pest species *A. proletella*, *B. brassicae* and *P. xylostella* from the beginning of sampling in early June. The first syrphid eggs and larvae were recorded in late June. Colonisation by all four groups peaked in July (Fig. 1.4), and *B. brassicae* and *P. xylostella* peaked again in October when colonisation by *A. proletella* and syrphids was negligible.

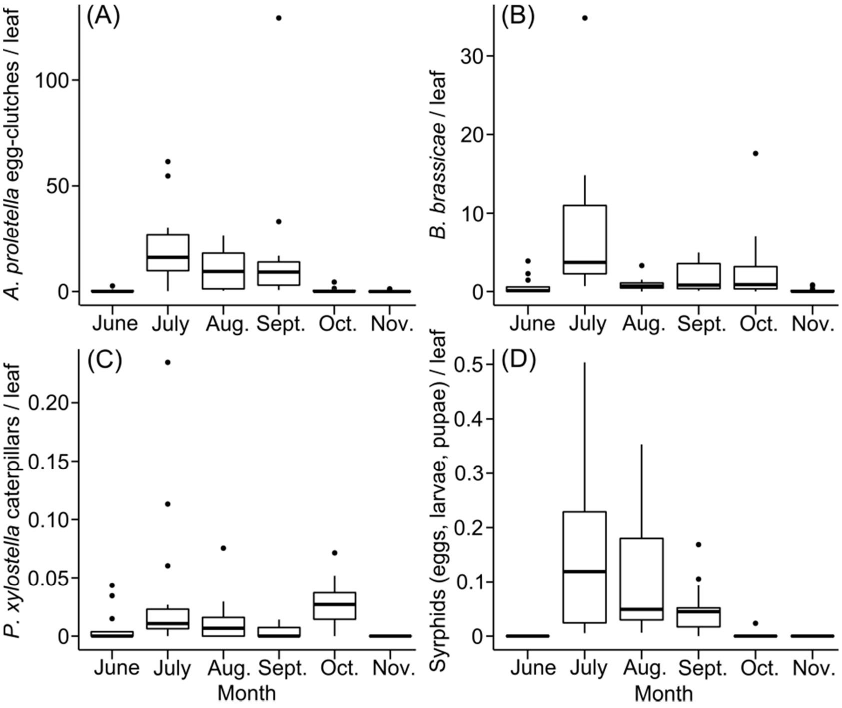

Fig. 1.4 Colonisation of monitoring plants throughout the season by (A) *Aleyrodes proletella*, (B) *Brevicoryne brassicae*, (C) *Plutella xylostella* and (D) syrphids. June: n = 12 study sites, July – November: n = 15 study sites.

3.2. Pests and syrphids in oilseed rape

Only adult *A. proletella* were found frequently on young oilseed rape in October and November, whereas all *A. proletella* developmental stages occurred frequently on maturing oilseed rape in June and July (Table 1.1). Finding exuviae of the fourth whitefly larval stage in July indicated that *A. proletella* could complete at least one generation in oilseed rape fields. *B. brassicae* was found only occasionally in oilseed rape fields throughout the year, whereas *P. xylostella* caterpillars and pupae were rarely found in June and July but more often in October and November. Syrphid eggs and larvae were generally rare in oilseed rape fields.

3.3. Land use

Cereals were the most widespread crops (11 % – 61 % of the landscape within 1 km radius around the study sites). Other frequent land use types were settlement area and grassland, followed by maize (Fig. 1.2). Oilseed rape, most likely affecting insect colonisation of *Brassica* vegetables, comprised 0 % – 12 % of the landscape within a 1 km radius. Forests, vegetables and sugar beets rarely reached 10 % of the landscape area (Fig. 1.2). The percentages of the different land use categories were similar among the different spatial scales (radii of 500, 750 and 1,000 m).

Table 1.1 Number of oilseed rape fields harbouring pests and natural enemy groups. n = number of fields sampled. No oilseed rape fields were present in August and September.

Month	*A. proletella*	*B. brassicae*	*P. xylostella*	Syrphids	n
June	11	2	1	1	11
July	12	6	2	3	14
October	11	5	5	0	14
November	13	6	5	1	14

3.4. Weather conditions

Southern and western wind directions (SE, S, SW, W and NW) were dominant during the day at all study sites. The prevailing winds came from the southwest at 12 of 15 study sites (80 %), whereas wind came least frequently from north at nine study sites (60 %). None of the wind directions dominated at night, further it was calmer than during the day (42 % records with no wind moving at night compared to 4 % during the day). Temperatures were 7.3 °C – 32.3 °C (mean, 19.9 °C) during the day and 5 °C – 24 °C (mean, 14.7 °C) at night.

3.5. Effects of land use and weather conditions on colonisation of monitoring plants

3.5.1. Cabbage whitefly (*Aleyrodes proletella)*

A single model explained the variance in colonisation by *A. proletella* best ($R^2 = 0.66$). The model showed a highly significant positive effect of oilseed rape area in the 1,000 m radius around the study sites when oilseed rape area was upwind weighted ($p = 0.001$, Table 1.2). The model also included a significant negative effect of temperature ($p = 0.011$).

3.5.2. Cabbage aphid (*Brevicoryne brassicae)*

The two best models for *B. brassicae* explained 32 and 44 % of the variance in colonisation (Table 1.2). Both included significant positive effects of downwind weighted oilseed rape area in a 1,000 m radius.

3.5.3. Diamondback moth (*Plutella xylostella)*

Five models explained the variance in colonisation of *P. xylostella* best (13 % – 24 % explained variability, Table 1.2). The very best model showed a marginally significant negative effect of downwind weighted area of ‘crop fields other than oilseed rape’ ($p = 0.06$). The second best model showed a marginally significant positive effect of downwind weighted area of permanent habitats ($p = 0.09$). Both landscape variables were highly correlated ($R^2 = 0.93$, $p < 0.001$). The remaining three models contained effects of ‘crop fields other than oilseed rape’ and permanent habitats but with $p > 0.1$.

3.5.4. Syrphids

The two best models for syrphids explained 43 % – 50 % of the variance in Brussels sprouts colonisation (Table 1.2). Both models contained a highly significant positive effect of prey abundance. The most abundant potential prey items were *A. proletella* egg clutches (38.4 %), followed by *A. proletella* larvae (37.6 %) and *B. brassicae* aphids (18.3 %). Prey abundance varied between 2.4 and 90.1 prey individuals / leaf (median, 42.9 prey individuals / leaf). The effects of landscape variables were not significant. However, we did not include the full set of variable combinations because of multicollinearity of variables (omitting combinations of prey abundance and oilseed rape area in a 1,000 m radius with and without weighting by wind; Appendix A Table A.4).

Table 1.2 Models for the effects of land use and weather conditions on *Aleyrodes proletella* (AP), *Brevicoryne brassicae* (BB), *Plutella xylostella* (PX) and syrphids (S) within a range of ΔAICc ≤ 2. Wind = weighting by wind; Est. = estimate; OSR = oilseed rape; Perm = permanent habitats (settlement, grassland and forest); OAC = other annual crop fields than oilseed rape (mainly cereals, maize, vegetables and sugar beets); Up / Down = upwind / downwind weighted habitats; - = parameter not included in the best models; x = parameter not tested.

Taxon	Land use	Radius (m)	Wind	Landscape		Temperature		Prey abundance		Overall model		
				Est.	p	Est.	p	Est.	p	p	R^2	ΔAICc
AP	OSR	1,000	Up	0.259	0.001	-0.024	0.001	x	x	0.001	0.66	0.00
BB	OSR	1,000	Down	0.117	0.027	-	-	x	x	0.027	0.32	0.00
BB	OSR	1,000	Down	0.110	0.030	0.015	0.149	x	x	0.032	0.44	1.10
PX	OAC	1,000	Down	-0.002	0.065	-	-	x	x	0.065	0.24	0.00
PX	Perm	1,000	Down	0.001	0.095	-	-	x	x	0.095	0.20	0.74
PX	OAC	750	Down	-0.001	0.115	-	-	x	x	0.115	0.18	1.11
PX	OAC	1,000	no	-0.001	0.117	-	-	x	x	0.117	0.18	1.15
PX	Perm	1,000	no	0.001	0.187	-	-	x	x	0.187	0.13	1.99
S	-	-	-	-	-	-	-	0.003	0.008	0.008	0.43	0.00
S	Perm	500	Down	0.002	0.210	-	-	0.003	0.005	0.020	0.50	1.78

4. Discussion

This study aimed to identify the effects of landscape elements and weather conditions on colonisation of Brussels sprouts by pests and natural enemies. Thereby, we investigated the effects of percentage area of oilseed rape, other annual crop fields and permanent habitats as potential source habitats within different radii around the study sites (500, 750 and 1,000 m radii). As hypothesised, oilseed rape, the most widespread agricultural *Brassica* crop, significantly affected colonisation of Brussels sprouts by investigated pest species, particularly under upwind or downwind weighting of habitats. The high importance of upwind source habitats pointed towards wind dispersal, whereas the high importance of downwind source habitats indicated olfactory oriented upwind flights.

4.1. Cabbage whitefly (*Aleyrodes proletella*)

According to our hypothesis, the occurrence of *A. proletella* on monitoring plants was strongly positively related to oilseed rape area. Furthermore *A. proletella* frequently occurred in winter oilseed rape fields in autumn and early summer, indicating that oilseed rape fields are important source habitats for colonisation of Brussels sprouts (see also Richter & Hirthe, 2014b; Ludwig & Meyhöfer, 2016). *A. proletella* uses winter oilseed rape as hibernation habitat and for reproduction in spring when vegetable *Brassica* crops are not available (Belder *et al.*, 2008). Exuviae of the fourth larval instar found in oilseed rape fields in early summer demonstrated that at least one generation can develop in oilseed rape fields. However, *A. proletella* adults are forced to move from oilseed rape fields during June and July, when maturing oilseed rape plants dry out and drop their leaves. This decline in host quality during late June and July explains why peak colonisation of vegetable *Brassica* crops occurred in early July and not at oilseed rape harvest in early August (Richter & Hirthe, 2014b).

The radius that explains most of the variance is supposed to represent the main dispersal distance of the studied species when the explanatory power of different models considering different landscape radii is compared (Schmidt *et al.*, 2008). The variability in the colonisation of monitoring plants was explained best by the oilseed rape area on the largest investigated scale (1,000 m radius). Thus, our results suggest that dispersal by *A. proletella* covers distances of at least 1,000 m. No references for *A. proletella* are available, but other whitefly species (*Trialeurodes vaporariorum* and *Bemisia tabaci*) are reported to perform migratory flights covering 500 – 1,000 m (Bährmann, 2002). Byrne *et al.* (1996) report peak *B. tabaci* migration 2 km from the source but also dispersal of 7 km has been reported (Cohen *et al.*, 1988). In accordance with our hypothesis, the explained variation increased when oilseed rape area was upwind weighted. This corresponds with the finding that whitefly dispersal is characterised by passive downwind transport (Byrne *et al.*, 1996).

Surprisingly, temperature had a negative and not a positive effect on colonisation by *A. proletella*. The movement activity of *A. proletella* increases with temperature to a peak at 27 °C and decreases at higher temperatures (Stein, 1958). Our weather recordings showed a mean daytime temperature of 19.9 °C, but 90 % of daytime records remained < 27 °C. Therefore, it is unlikely that the negative temperature effect on colonisation resulted from decreasing flight activity at temperatures > 27 °C. Temperature has a positive effect on *B. tabaci* abundance in trap heights of 7.2 m, whereas catches at lower heights remain unaffected (Isaacs & Byrne, 1998), as shown in melon fields in Arizona, USA. Consequently, whitefly dispersal may be affected by vertical and horizontal air movements. Thermal columns of rising air may frequently occur above sparsely covered soil of vegetable fields on warm days in early summer. This rising air can lift the whiteflies, preventing them from landing on host plants, particularly on warm days. However, this explanation for the negative temperature effect on colonisation by whiteflies is speculative and needs further investigation.

4.2. Cabbage aphid (*Brevicoryne brassicae)*

Downwind weighted oilseed rape area in a 1,000 m radius was the most important variable in explaining *B. brassicae* colonisation of monitoring plants. Overwintering *B. brassicae* are often found in oilseed rape fields (Hafez, 1961; Collier & Finch, 2007). However, they were detected only occasionally in oilseed rape fields in our study. This low abundance is consistent with the comparably weak effect of oilseed rape area. The difference in *A. proletella* and *B. brassicae* abundance may be due to different sensitivities to insecticides. First, *B. brassicae* is often found highly exposed on the stem of oilseed rape plants, whereas *A. proletella* is more sheltered on the lower side of leaves. Second, pyrethroids, which are usually sprayed in oilseed rape fields in October and March, affect *B. brassicae* populations (Alford *et al.*, 2003) and pyrethroid resistance has only been reported in Asian countries (Ahmad & Akhtar, 2013). In contrast, *A. proletella* developed resistance at least in some parts of Europe (Springate & Colvin, 2012).

Downwind weighted oilseed rape area explained the variability in colonisation best, suggesting that *B. brassicae* located their hosts by upwind movement. Aphids are seen as weak fliers, unable to cope with headwinds > 0.5 m/s and are dispersed downwind for large distances (Kring, 1972). However, upwind flights towards optical or olfactory stimuli are reported (Döring, 2014). Several aphid species use olfactory cues to locate hosts (Webster, 2012), but for *B. brassicae* results on the reaction on odours differ (Nottingham *et al.*, 1991; Nottingham & Hardie, 1993). The scale on which olfactory cues are used to determine the location of host plants is still unknown (Döring, 2014). Dispersing *B. brassicae* fly for about two hours (Kring, 1972). As aphids fly at 0.4 – 0.9 m/s (1.3 – 3.2 km/h), they can cover 1,000 m in that time (Kring, 1972). Our finding that downwind weighted oilseed rape area explained the variability in colonisation better than oilseed rape area without weighting by wind is the first report that aphids are attracted upwind over a surprisingly large distance of about 1,000 m.

4.3. Diamondback moth (*Plutella xylostella*)

Downwind weighted permanent habitats in a 1,000 m radius showed a positive, and downwind weighted annual crops in a 1,000 m radius a negative marginal significant effect on colonisation by *P. xylostella*. Both variables were highly negatively correlated ($R^2 = 0.93$, $p < 0.001$) and their effects could not be separated. Landscapes with a low proportion of annual crops and high proportion of permanent habitats, including grasslands and gardens, may provide more nectar as food for adult *P. xylostella,* leading to high colonisation of host plants (Winkler *et al.*, 2005). Surprisingly, the amount of oilseed rape in surrounding landscapes had no significant effect on this *Brassica* pest species, probably because it was already fruiting during July when field survey took place. Similarly, other studies have shown no effect of the quantity of oilseed rape on damage by *Brassica* pests whose adults depend on floral resources such as *Delia radicum* and *Meligethes aeneus* (Thies & Tscharntke, 1999; Josso *et al.*, 2013). Furthermore, permanent habitats may be suitable overwintering habitats, although the overwintering strategy of *P. xylostella* in temperate regions remains uncertain and at least part of the population immigrates from warmer regions (Talekar & Shelton, 1993). As *P. xylostella* uses olfactory cues to locate hosts (Pivnick *et al.*, 1994), permanent habitats in downwind direction may have been important for *P. xylostella* colonising the monitoring plants (Moser *et al.*, 2009).

4.4. Syrphids

No effects of oilseed rape, other annual crops or permanent habitats were detected regarding colonisation of monitoring plants by syrphids. Aphidophagous syrphids use different habitats during different life stages. Adults are highly mobile and require flower-rich habitats as source of nectar and pollen to supply energy for flight and protein for egg development (Haslett, 1989). The effects of oilseed rape fields on syrphids may be limited to their flowering time in April/May (Riedinger *et al.*, 2014). Adults move to other habitats after oilseed rape flower (Meyer *et al.*, 2009). Crop fields are of importance for egg deposition and larval development, as they provide large amounts of food for larvae (Meyer *et al.*, 2009). Syrphids hibernate in different habitats, such as crop fields or grasslands (Raymond *et al.*, 2014; Sarthou *et al.*, 2014), while some important aphidophagous syrphids are at least partially migratory and independent from local habitats (Raymond *et al.*, 2013). High mobility and different habitat requirements of syrphids probably led to no significant landscape effects.

Instead, colonisation of monitoring plants by syrphids was strongly affected by prey abundance, which was dominated by *A. proletella* (88 %). Syrphids are important natural enemies of aphids (Tenhumberg & Poehling, 1995). *E. balteatus*, the most common syrphid species in Brussels sprout fields in Germany (Hafez, 1961), is known to also feed on whiteflies and to develop into an adult while feeding on whiteflies only (Rijn *et al.*, 2008). Different syrphid species, including *E. balteatus,* are attracted by honeydew and pheromones from particular aphid species (Budenberg & Powell, 1992; Verheggen *et al.*, 2008). Rijn *et al.* (2008) reported increased egg laying by syrphids on plants with whiteflies compared to clean plants. These reports are supported by the strong positive effect of prey abundance on colonisation by syrphids in our study.

4.5. Conclusion

The effects of different land use types and weather conditions on colonisation of young Brussels sprout plants by *Brassica* pests and natural enemies were species specific. As expected, oilseed rape as most widespread agricultural *Brassica* crop was an important source habitat for *A. proletella* and *B. brassicae*. In contrast, colonisation by *P. xylostella* increased with area of permanent habitats, possibly due to consistent floral resources for nectar-feeding adults and was unaffected by oilseed rape farming. Syrphids were significantly affected by prey abundance, but not by tested land use types probably due to their high mobility and miscellaneous habitat requirements.

The effect of oilseed rape area on colonisation by *A. proletella* increased when additional weight was given to upwind located habitats, pointing towards downwind dispersal of this species. In contrast, the effect of oilseed rape area on colonisation by *B. brassicae* increased when additional weight was given to downwind located habitats, suggesting that this species follows olfactory cues of host plants upwind. These findings emphasise the importance of considering prevailing wind directions when investigating or predicting colonisation by pest species, which probably also applies to other arthropods, including natural enemies such as ballooning spiders and pollinators such as moths and bees (Wright & Schiestl, 2009).

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Chapter 2

Cabbage whiteflies colonise *Brassica* vegetables primarily from distant, upwind source habitats

Martin Ludwig, Hella Schlinkert, Christopher Conrad, Thorsten Dahms & Rainer Meyhöfer

Abstract

The occurrence of species in rapidly changing environments, such as agricultural landscapes, is largely affected by their ability to recolonise habitats. Knowledge of the scale of importance for colonisation processes is essential for landscape-scale management of wildlife populations, e.g. pest management strategies. Colonisation by many insects, such as whiteflies, can be affected on multiple landscape scales, as they have different morphs with specific dispersal abilities and behaviours. The cabbage whitefly (*Aleyrodes proletella*) is a major pest of *Brassica* vegetables and is known to colonise them primarily from oilseed rape fields. We used field mapping and remote sensing to characterise the relevant scales for colonisation of Brussels sprouts by cabbage whiteflies. Surprisingly, oilseed rape areas in wide landscapes (2 – 8 km around study sites) explained colonisation remarkably better than oilseed rape areas at the local scale (200 – 1,000 m around study sites). The explained variance increased when additional weight was given to upwind source habitats, indicating wind transport of whitefly colonisers and consequently explaining the importance of large landscape scales for colonisation. Relatively low importance of local compared to wide landscape source habitats can be explained by the specific flight behaviours of different whitefly morphs. Migratory morphs show phototactic attraction but are attracted by host cues only during the later phases of flight. Therefore, they ignore potential host plants close to their place of origin and disperse several kilometres. Trivial flight morphs rarely move more than a few hundred metres. In conclusion, as most whitefly colonisers reached *Brassica* vegetables from source habitats as far away as 2 – 8 km, predictions on pest pressure and landscape-scale whitefly management should consider these distances. In contrast, oilseed rape fields in the local landscape, which usually worry farmers, have a relatively negligible effect on colonisation pressure.

Key words: *Aleyrodes proletella*, wind dispersal, landscape scale pest management, Brussels sprout, satellite image, remote sensing, spillover, landscape configuration

1. Introduction

Colonisation processes impact species communities, including pest outbreaks and species survival, particularly in rapidly changing habitats, such as agricultural landscapes (Wissinger, 1997; Tscharntke *et al.*, 2005). Dispersal is a major driver of colonisation and defined as the movement of organisms away from their parental source to other locations (Lewis *et al.*, 2013). It thereby includes movement within as well as among populations and habitats, thus, movement on different scales. In terms of insect flights, so-called ‘trivial flights’ can be distinguished from ‘migratory flights’ (Johnson, 1969; Danthanarayana, 1986). Trivial flights, also called vegetative or appetitive flights, are random short distance flights usually associated with feeding, mating or oviposition behaviour inside habitats (Danthanarayana, 1986). In contrast, migratory flights cover relatively long distances and are, with exception of the late phase of flight, undistracted by stimuli referred to everyday (‘trivial’) needs (Johnson, 1969). Migratory flights are often associated with switches among and colonisation of new habitats (Danthanarayana, 1986). Knowledge on the spatial dimension, in which dispersal affects colonisation, is important for management of wild animal populations regarding subject areas such as conservation, utilisation or crop protection (Mazzi & Dorn, 2012).

In this study, we investigated colonisation of young Brussels sprout plants by the cabbage whitefly (*Aleyrodes proletella*), a serious pest in *Brassica* vegetable fields, such as kale, Savoy cabbage and Brussels sprouts (Pelgrom *et al.*, 2015). The cabbage whitefly prefers Brassicaceae plants but also occurs less frequently on plants in the families Asteraceae and Papaveraceae (Bährmann, 2002). The worldwide spread of cabbage whitefly and its importance as a vegetable pest have increased dramatically in the last few decades (El-Helaly *et al.*, 1972; Barro & Carver, 1997; Pelgrom *et al.*, 2015). Furthermore, the species has developed resistance to pyrethroid insecticides (Springate & Colvin, 2012). The increasing abundance of cabbage whiteflies in Europe may be related to increased production of oilseed rape in the last few decades (Dixon, 2007). Cabbage whiteflies use winter oilseed rape fields as hibernation and spring reproduction habitat when *Brassica* vegetables are unavailable (‘green bridge’; Dixon, 2007; Belder *et al.*, 2008). In early summer, when oilseed rape fields mature, whiteflies disperse to the surrounding landscape due to the decrease in host quality (Richter & Hirthe, 2014b). At this time of the year, newly planted *Brassica* vegetables are available as alternative hosts. Therefore, oilseed rape fields are an important source for colonisation of *Brassica* vegetable fields by the cabbage whitefly (Richter & Hirthe, 2014b).

Dispersal ability largely determines the relevant scale for colonisation processes. Whiteflies have been traditionally seen as weak flyers, unable to actively fly more than few hundred metres (Byrne & Bellows, 1991). Thus, the availability of source habitats within the local landscape seems to be the key factor for the successful colonisation of a habitat and colonisation built up. Accordingly, oilseed rape area in up to 1,000 m distance affects colonisation by cabbage whiteflies (Ludwig & Meyhöfer, 2016; chapter 1). However, the importance of more distant source habitats is unknown. Studies on the silverleaf whitefly (*Bemisia tabaci*) show a bimodal dispersal pattern with peaks at 100 and 2,000 m distances from the dispersal source (Byrne *et al.*, 1996). Byrne *et al.* (1996) concluded that the different peaks of the silverleaf whitefly result from two morphs differing in their specific ability and willingness to fly, namely from the so-called ‘trivial flight morph’ (100 m peak) and from the ‘migratory flight morph’ (2,000 m peak). Migratory and host finding behaviour of aphids and whiteflies is similar. During migratory flights they are attracted by UV- or white skylight and thereby ignore host cues (Isaacs *et al.*, 1999; Döring, 2014). Subsequent host finding is similar to behaviour during trivial flights and characterised by attraction to green to yellow surfaces (Blackmer *et al.*, 1994; Isaacs *et al.*, 1999), while some species additionally respond to olfactory cues (Butler, 1938; Döring, 2014). Finally, host suitability is tested by probe sucking after landing (Noldus *et al.*, 1986).

Similar to the silverleaf whitefly also the cabbage whitefly has different morphs with specific flight abilities (Iheagwam, 1977). Consequently, cabbage whiteflies colonising *Brassica* vegetables may either (1) be migratory morphs derived from source habitats (particularly oilseed rape fields) up to several kilometres away or (2) trivial flight morphs derived from source habitats in the local landscape of a few hundred metres distance. Upwind source habitats should be of utmost importance for wind-dispersed migratory morphs to colonise *Brassica* vegetables (Naranjo *et al.*, 2010). In contrast, colonisation by trivial flight morphs should either be independent of prevailing wind directions as they fly in calm conditions close to the ground and find their hosts by random landing on green surfaces and probing (Byrne & Bellows, 1991), or downwind source habitats should be of the highest importance, if cabbage whiteflies follow olfactory cues (Fig. 1.1; Butler, 1938; Pasek, 1988; Bleeker *et al.*, 2009). Consequently, colonisation by whiteflies might be affected simultaneously on multiple landscape scales.

1.1. Questions and hypotheses

To answer the question in which landscape radii oilseed rape area mainly affects colonisation of Brussels sprouts by cabbage whiteflies, the variance explained by individual landscape radii (200 – 8,000 m) was compared.

First, we hypothesised that colonisation of *Brassica* vegetables by the cabbage whitefly depends on the amount of oilseed rape as a source habitat in the local landscape, due to the typical dispersal behaviour by trivial flights, as well as in the wide landscape, due to migratory flights. Therefore, a model simultaneously considering oilseed rape area at these two different spatial scales should explain the colonisation pattern better than a model considering only one of these scales. As the exact distance covered by cabbage whiteflies in trivial and migratory flights is unknown, different radii for the local (200 – 1,000 m) and wide landscapes (1,000 – 8,000 m) were tested.

Second, we hypothesised that downwind transport is of importance for dispersal on wide landscape scale. Thus, giving additional weight to upwind source habitats at the wide landscape scale should increase the model's explanatory power.

Third, we hypothesised that olfactory orientation towards host plants plays a role in trivial flights by the cabbage whitefly. Consequently, giving additional weight to downwind source habitats at the local landscape scale should further improve the model's explanatory power.

2. Methods

2.1. Field survey

Eighteen Brussels sprout fields on organic horticultural farms located in northwest North Rhine-Westphalia and southern Lower Saxony, Germany, were selected. Farmers grew a large variety of vegetables, including Brussels sprouts (planted from late April to early June) and other *Brassica* vegetables. The agricultural landscape surrounding the study site (Brussels sprout fields) differed in land use and represented a gradient in the area of oilseed rape, e.g. 0 to 20 % and 0.5 to 11 % oilseed rape at 200 and 8,000 m radii around the study sites, respectively. A weather station (PCE-FWS 20; PCE Instruments, PCE Deutschland GmbH, Meschede, Germany) recorded wind directions at 15 minutes intervals on each study site.

Colonisation of Brussels sprouts by cabbage whiteflies was sampled on monitoring plants exposed at all study sites in early July 2012 at the peak of cabbage whitefly early summer migration (Ludwig *et al.*, 2014, chapter 1). Monitoring plants were potted organically cultivated Brussels sprout plants free of pests and natural enemies. They were standardised in terms of soil type (mixture of 1.7 g water storing granulate [Broadleaf P4, AgriPol, Bournmoor, England] per litre potting soil), age (3 – 4 weeks), variety (*Brassica oleracea* var. *gemmifera,* cultivar 'Topline F1') and were selected randomly from stock. Twenty monitoring plants were exposed per study site in 0.5 - 5 m distance from the farmer's Brussels sprout plants. The plants were placed in two groups of ten plants each, preferably on two different sides of a field to account for spatial heterogeneity on the field. After 2 weeks eggs and larvae of cabbage whiteflies were counted on all leaves of the monitoring plants.

2.2. Landscape survey by manual mapping and remote sensing

To quantify the position and area covered by oilseed rape fields in 8 km radii around study sites, we manually mapped the local agricultural landscape (1 km radius) around study sites and used relatively less time-consuming remote sensing methods to assess land use in radii from 1 to 8 km. Manually mapping of land use types took place on site by car and foot using aerial photos (scale: 1:10,000). Agricultural land use types were thereby grouped in ten crop type classes (Appendix B Table B.1.1). These data, in addition to forest and urban areas mapped on the basis of satellite images, were digitised using ESRI ArgGIS 10 (Environmental Systems Research Institute, Redlands, Californien, USA).

In a further step, these results were used as reference data to determine land use in the wide landscape (up to 8 km) using satellite images and remote sensing methods. Therefore the reference data objects were separated into training data (70 %) to train the classification algorithm 'Random Forests' and holdout (30 %) for final validation of the classification (Breiman, 2001; Appendix B Table B.1.1). 'Random Forests' is a machine learning method that is widely used to classify remote sensing data (Pal, 2005) including the identification of different crops (Conrad *et al.*, 2014).

The classification of pixel-based satellite image units into land use types was performed as follows: Five Landsat 7 ETM+ scenes were used for the classification (acquisition DOYs in 2012: 66, 146, 199, 247 and 279). Clouds were masked out using a threshold on the blue band and the 'Normalised Differenced Vegetation Index' (NDVI). As classifications do not require an atmospheric correction (Song *et al.*, 2001), this step was applied to the top-of-atmosphere reflectance data. Four spectral bands (blue, green, red and near-infrared), as well as the vegetation indices 'Soil-adjusted Vegetation Index' (SAVI), NDVI and the 'Simple Ratio'

(SR) were utilised as input for the classification (Appendix B Table B.1.2). Due to cloud coverage and the ‘Scan Line Correction error’ (SLC) (Wulder *et al.*, 2014), we classified and merged multiple Landsat scene combinations to cover the entire study area. In the final class decision for a single pixel, the classification with more input scenes was prioritised over the classification based on fewer Landsat scenes to ensure that the full potential of the multi-temporal dataset was used and that the major part of the study area was classified. The resulting post-classification map was clumped using ‘ENVI’ version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado, USA) to ensure spectral coherency.

The final land cover map was validated using the holdout described above. The classification accuracies were calculated according to Congalton (1991) and are shown in Appendix B Table B.1.3. Overall accuracy was 79.89 % (Kappa coefficient = 0.76), whereas the accuracies of the class of interest (oilseed rape) were higher (producer’s accuracy = 89.51 % and user’s accuracy = 88.96 %; Appendix B Table B.1.3). The landscape classification resulted in maps with compact, often rectangular cropland units (Appendix B Fig. B.1), which can be seen as additional proof of the accurate classification results.

2.3. Data preparation

As recording wind data failed at two of the 18 study sites and no remote sensing landscape data were available from another study site, all data analyses were conducted with 15 of the initial 18 study sites. The mean number of egg clutches laid per leaf within a 2 week exposure time at each study site was used as a measure of colonisation. Thereby, egg clutches that hatched during the exposure time were included (4.678 larvae corresponded to one clutch; chapter 1, Appendix A Fig. A.3).

The percentage area covered by oilseed rape within circular areas around the study sites was calculated at 16 radii ranging from 200 to 1,000 m in 100 m steps (local landscape) and from 1,000 to 8,000 m in 1,000 m steps (wide landscape) to investigate the importance of oilseed rape fields as source habitats at different radii. Data recorded by personal mapping were used to ensure the highest accuracy for the nine local landscape radii, whereas the data obtained from satellite image analysis were used for the eight wide landscape radii, allowing us to consider the large-scale landscapes (which could not be mapped manually). The data generated from the satellite images at the 1,000 m radius and those from personal mapping were highly correlated ($R^2 = 0.84$, $p < 0.001$).

To weigh the contribution of the oilseed rape areas according to their location relative to the study site and prevailing wind directions, the circular landscape areas were separated into eight wind direction sectors (N, NE, E, SE, S, SW, W and NW; Fig. 2.1). To account for a greater importance of upwind source habitats in cases of passive wind dispersal, we first calculated the proportion of wind events (> 0.3 m/s) blowing from each of the eight sectors towards the study site during the time the monitoring plants were exposed. Second, the percentage oilseed rape area per sector was multiplied by the proportion of wind events blowing towards the study site. The sum of the resulting eight values (one value per sector) produced an area index with increased weight for upwind located habitats, hereafter referred to as 'upwind weighted' area (Appendix B Table B.2). To account for a greater importance of downwind source habitats in cases of attraction by wind-transported odours, we weighted the area of the three habitat categories accordingly: The percentage oilseed rape area per sector was multiplied by the proportion of wind events blowing from the study site towards the sector. The sum of these resulting eight values (one value per sector) produced an area index with increased weight for downwind located habitats, hereafter referred to as 'downwind weighted' area.

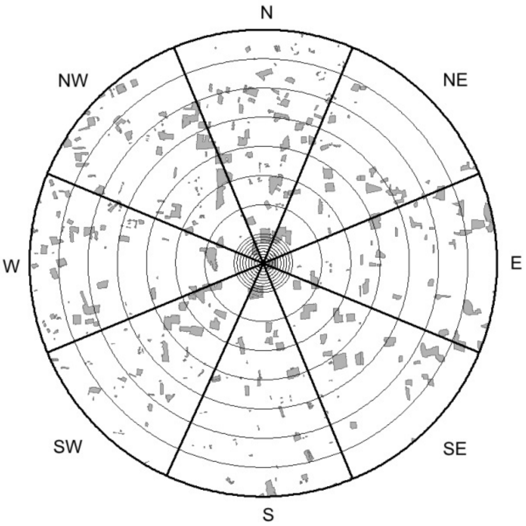

Fig. 2.1 Separation of one of the analysed landscapes into circular areas with different radii around the study site (thin grey circles) and sectors dedicated to wind direction (differrentiated by bold black lines). Grey areas represent oilseed rape fields.

2.4. Statistics

Regression models were used to analyse the effects of oilseed rape area at different scales with and without weighting by wind on colonisation of Brussels sprout. The number of *A. proletella* egg clutches was used as a response variable in all models and was log-transformed to account for the non-normally distributed count data. To identify landscape radii in which oilseed rape mainly affected colonisation by pests, we calculated 34 models containing one of the 34 explanatory variables (nine radii from 200 m to 1,000 m for the local scale once with and once without downwind weighting of oilseed rape area and eight radii from 1,000 m to 8,000 m for the wide scale once with and once without upwind weighting of oilseed rape area). To investigate whether including two spatial scales explained colonisation better than one scale, we calculated models with two explanatory variables (percentage oilseed rape area on the local and wide scales) covering all possible combinations of local-scale (nine radii) and wide-scale radii (eight radii). Thereby, the combinations with correlated explanatory variables were excluded (Appendix B Table B.3), leading to a total of 65 models. Furthermore, we calculated 194 models in which one or both variables were weighted by wind (again excluding combinations with correlated explanatory variables). All of these models (34 + 65 + 194 = 293) were ranked using Akaike Information Criterion corrected for small sample size (AICc), which is a measure of relative goodness-of-fit and simplicity of the statistical models for a given data set. The best models in a range of delta AICc ≤ 2, which are supposed to be of similar quality (Burnham & Anderson, 2002), are shown. All analyses were performed using R version 3.3.1 (R Core Team, 2016).

3. Results

The cabbage whitefly was the most abundant pest species on Brussels sprout plants and density reached 0.2 – 61.4 egg clutches/leaf (median = 15.3, mean = 19.4). No natural enemies specialised on whiteflies (e.g. chalcid wasp *Encarsia tricolor* or lady beetle *Clitostethus arcuatus*) were observed, but syrphid larvae and spiders were present. Due to the absence of specialised natural enemies and the general weak effects of natural enemies on cabbage whiteflies (Rijn *et al.*, 2008), they were not considered in the analyses. The prevailing wind directions were southern or western directions (SE, S, SW, W and NW) for all study sites. The most frequent wind direction was southwest at 12 of the 15 study sites (80 %), whereas north was the direction with the least wind at nine study sites (60 %).

A comparison of the explained variance (R^2) of the models that included oilseed rape area on single scales showed two peaks (Fig. 2.2): the first peak marked a moderate explained variance at the smallest landscape radius (200 m with $R^2 = 0.12$), where colonisation increased with decreasing oilseed rape area. The second peak marked the highest explained variance at the 5,000 m radius ($R^2 = 0.36$), with a steep increase in explained variance from 700 to 2,000 m. Here colonisation of Brussels sprouts increased as oilseed rape area increased.

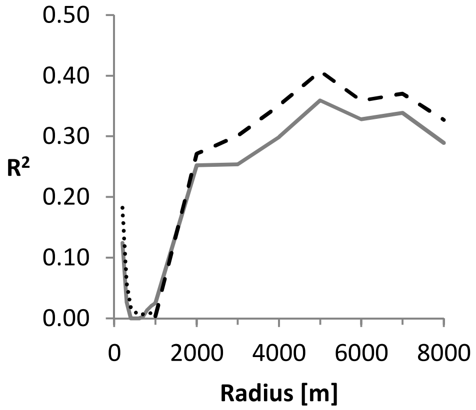

Fig. 2.2 Explained variance (R^2) of cabbage whitefly colonisation of Brussels sprouts by the percentage of oilseed rape area (i.e. source habitat) in 17 radii resulting from separate models for each radius. Continuous grey line = local and wide landscape scale without weighting by wind, dashed black line = wide scale landscape with upwind weighted oilseed rape area, black dotted line = local scale landscape with downwind weighted oilseed rape area.

After comparing all combinations of oilseed rape area at the wide-scale and/or local-scale landscapes with and without weighting by wind, eight of the total 293 models were in the $\Delta AICc \leq 2$ range (Table 2.1). All of these models showed a significant effect of oilseed rape area at the wide scale, but local scale landscapes were not included in any of these best models.

Five of the eight best models for the wide landscape scale contained upwind weighting of source habitats, including the model with the lowest AICc (5,000 m radius with upwind weighting of oilseed rape area, $R^2 = 0.41$, $p = 0.011$). The comparison of variance explained by models with oilseed rape area in different radii with and without weighting by wind as a single explanatory variable showed that upwind weighting of oilseed rape area on a wide landscape scale increased the explained variance of all scales with a radius ≥ 2,000 m (Fig. 2.2). Downwind weighting of oilseed rape area on local landscape scale increased explained variance only at the 200 m radius.

Table 2.1 Models in a ΔAICc ≤ 2 range for colonisation of young Brussels sprout plants by cabbage whiteflies. AICc = Akaike Information Criterion corrected for small sample size. wei = weighting of oilseed rape area by wind direction, + = with weighting, - = without weighting, est = estimate. Oilseed rape area was upwind weighted on the wide landscape scale (2,000 – 8,000 m radius) and downwind weighted on the local landscape scale (200 – 1,000 m radius). Empty cell = variable was not part of the model.

Wide landscape scale				Local landscape scale				Overall model		
radius	wei	est	p	radius	wei	est	p	p	R^2	ΔAICc
5000	+	0.176	0.011					0.011	0.41	0.00
7000	+	0.194	0.016					0.016	0.37	0.90
5000	-	0.171	0.018					0.018	0.36	1.17
6000	+	0.178	0.018					0.018	0.36	1.17
4000	+	0.152	0.020					0.020	0.35	1.35
7000	-	0.191	0.023					0.023	0.34	1.63
6000	-	0.177	0.026					0.026	0.33	1.87
8000	+	0.187	0.026					0.026	0.33	1.90

4. Discussion

Our results show that the area of oilseed rape fields (source habitats), within a 5,000 m radius from the study sites, explained 36 % of the variance in colonisation of young Brussels sprout plants by the cabbage whitefly. The explained variance increased (to a maximum of 41 %) when source habitats were upwind weighted. In contrast, oilseed rape area at the local landscape scale showed no or only a weak effect on colonisation of young Brussels sprout plants by the cabbage whitefly. These findings highlight the importance of source habitats on a wide landscape scale for even weak fliers such as whiteflies (Byrne & Bellows, 1991) and reveal the importance of passive downwind transport for dispersal.

The low proportion of explained variability in whitefly colonisation by oilseed rape area in the local landscape and the steep increase in explained variation from radii of 700 to 2,000 m suggest that landscapes up to 700 m play a negligible role, whereas landscapes ≥ 700 m are particularly important for whitefly colonisation. Accordingly, an analysis of ring-shaped landscape areas (i.e. when only landscape > 700 m from the study site was considered) showed almost the same results as those of the circle-shaped landscape with the corresponding radius (unpublished data). This leads to the question of why source habitats in a wide-scale landscape are more important for colonising *Brassica* vegetable fields compared to that of local-scale source habitats. A possible reason is that cabbage whitefly migratory morphs are the main colonisers of *Brassica* vegetable fields. Trivial flight morphs fly for a very short time only (19 seconds on average; Iheagwam, 1977) and immediately land on spotted green surfaces (Blackmer *et al.*, 1994). Therefore, they may only be able to reach a new habitat if it directly borders their source habitat. In our study, we did not detect colonisation by trivial flight morphs, as none of the studied Brussels sprout fields directly adjoined an oilseed rape field (the minimal distance was > 100 m with one exception of > 40 m but shielded by field hedges). In contrast, migratory whitefly morphs fly for 15 minutes on average (Iheagwam, 1977). They show positive phototactic behaviour and ignore visual host cues during the first phase of their flight (Iheagwam, 1977; Isaacs *et al.*, 1999), which can cover 2 – 7 km (Cohen *et al.*, 1988; Byrne *et al.*, 1996). This behaviour, which is similar to dispersal strategy of other insects such as aphids (Döring, 2014), can be meaningful in order to avoid exploitation of the local resources as consequence of population growth or decrease in resource availability. Consequently, most migratory morphs may not colonise Brussels sprout fields close to their source habitat, as their specific flying behaviour leads them directly to a height where they are transported by the prevailing wind. Thus, whitefly populations of the wide-landscape's oilseed rape fields may colonise Brussels sprout fields independently from whitefly populations in the local landscape.

Consequently, these results do not confirm our first hypothesis, stating that a model involving two spatial scales (considering the different morphs) explains colonisation by the cabbage whitefly better than a model considering only one spatial scale. All eight of our best models contained only wide-scale landscape variables, indicating that the wide landscape was the most important for colonisation of Brussels sprouts by cabbage whiteflies, whereas the local landscape seemed to be almost negligible.

The second hypothesis stated that wind transport is important for a wide-landscape scale dispersal of the cabbage whitefly and, consequently, models including upwind weighted oilseed rape area explain colonisation particularly well. Three of the eight best models considered oilseed rape area without weighting by wind; thus, there is no solid proof for high importance of wind effects during colonisation by cabbage whitefly. On the other hand, the models including upwind weighting of oilseed rape area always had a lower AICc and explained more variance than equivalent models without weighting by wind (Table 2.1, Fig. 2.2). The importance of wind transport in dispersal has been suggested previously for other whitefly species (Byrne *et al.*, 1996; Bährmann, 2002). Silverleaf whitefly dispersal can peak 2 km downwind from the source habitat while single individuals travel distances of 7 km (Cohen *et al.*, 1988; Byrne *et al.*, 1996). For aphids passive wind transport of even hundreds of kilometres is reported, while flights of < 20 km are seen as local movement (Loxdale *et al.*, 1993).

While optical orientation is most important, also olfactory orientation can be used by whiteflies to find host plants (Butler, 1938; Vaishampayan *et al.*, 1975; Bleeker *et al.*, 2009). Therefore, we hypothesised that cabbage whiteflies are attracted by Brussels sprout fields from nearby downwind located oilseed rape fields (which decrease in host plant quality while they mature). This hypothesis was not confirmed, as oilseed rape area at the local scale (200 m radius) had, if any, a negative effect on colonisation of Brussels sprout. In addition, the quality of oilseed rape host plants is generally weak in July but oilseed rape plants with delayed development (often found on lanes inside the fields) may be suitable cabbage whitefly hosts. Therefore, they may attract cabbage whiteflies that otherwise might have colonised Brussels sprout fields in landscapes with low oilseed rape area within the 200 m radius. The negative effect was even more pronounced when oilseed rape area was downwind weighted. A similar effect of decreasing colonisation with increasing downwind source habitat area was found for pollen beetles, which use olfactory cues to locate hosts (Moser *et al.*, 2009). The authors explained this effect by stating that lower numbers of herbivores reach a study site when alternative source habitats are along their way. However, the role of olfactory orientation is not well investigated in whiteflies. The most important host location cues for whiteflies are visual (Mound, 1962; Vaishampayan *et al.*, 1975), but olfactory stimuli affect pre-alighting host selection behaviour (Vaishampayan *et al.*, 1975; Bleeker *et al.*, 2009). The cabbage whitefly was found to orientate towards the scent of crushed cabbage leaves (Butler, 1938), but no orientation towards the scent of intact cabbage leaves could be detected (P. Hondelmann, pers. com.).

4.1. Conclusion

The combination of wind and landscape configuration data as well as determining the most important landscape scale (5,000 m radius) using satellite images in our study is an important step to successfully predict colonisation of cabbage plants by the cabbage whitefly. We combined wind and landscape configuration data by upwind weighting of source habitats (i.e. oilseed rape fields) on a wide landscape scale (assuming wind dispersal) and downwind weighting of source habitats on a local landscape scale (assuming olfactory orientation during host finding). The wide landscape radii of 2,000 – 8,000 m explained colonisation best, particularly when source habitats were upwind weighted, indicating wind transport by whitefly colonisers. Local landscapes (up to 1,000 m radius) were only slightly important for colonisation by cabbage whiteflies. This was explained by the specific flight behaviour of migratory morphs, ignoring potential host plants close to their place of origin and dispersing several kilometres. Thus, predictions on pest pressure and landscape scale whitefly management need to consider large landscape scales. In contrast, oilseed rape fields at distances up to 1,000 m, of which farmers usually are most concerned, are relatively negligible for colonisation. These predictions could be further refined by implementing other environmental factors, such as temperature or rainfall (Naranjo *et al.*, 2010, chapter 1) and may be useful to develop integrated plant protection strategies.

Apart from its relevance in crop protection, the combined use of wind and landscape effects is of interest for landscape ecological science, as they represent further development of the common nested circles method (Thies & Tscharntke, 1999). The combination of wind and landscape effects are useful to predict not only pest outbreaks but also colonisation by other arthropods affected by wind, either by downwind transport of small arthropods, such as aphids, whiteflies or ballooning spiders (Compton, 2002; Schmidt & Tscharntke, 2005), or for upwind oriented olfactory searchers, such as the pollen beetle or parasitoid wasps (Steinberg *et al.*, 1993; Moser *et al.*, 2009).

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Chapter 3

Efficacy of crop cover netting against cabbage pests and their natural enemies and relevance of oilseed rape

Martin Ludwig & Rainer Meyhöfer

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Abstract

Crop cover nets are used in vegetables to reduce damage by pests. Recently, nets with 0.8 mm mesh size were recommended to protect *Brassica* vegetables from whiteflies, but farmers doubted their efficacy. We compared the impact of different mesh sizes on the abundance of insect pests and their antagonists on Brussels sprouts in a field study and considered also important resource habitats, i.e. oilseed rape, in the surroundings. Cabbage whitefly was the most abundant pest followed by peach-potato aphid, cabbage aphid and diamondback moth. Aphid parasitism reached 48 % while syrphid larvae and spiders were the most abundant predatory taxa. The cabbage whitefly was less abundant under 0.8 mm nets in June and August compared to 7 mm nets, while no effect was observed in October. In general cabbage aphid, diamondback moth, syrphids and aphid parasitism were not affected by nets, but peach-potato aphid density increased under 7 mm nets late in the season. In contrast, spiders were less abundant under 0.8 mm than under 7 mm nets. Moreover, only the cabbage whitefly was positively affected by oilseed rape growing. In summary, 0.8 mm nets may be beneficial to reduce colonisation by cabbage whiteflies, especially in early summer and in landscapes with high colonisation pressure. Nets with wider mesh size may be appropriate in landscapes with low colonisation pressure by cabbage whiteflies since 0.8 mm mesh size had the disadvantages to support the peach-potato aphid and hinder colonisation by spiders.

Key words: net mesh size, *Aleyrodes proletella*, *Brevicoryne brassicae, Myzus persicae, Plutella xylostella,* hoverfly

1. Introduction

Crop cover is a preventive measure used in several vegetable crops to minimise damage by pests in integrated and organic farming. In *Brassica* crops, nets with a mesh size of 1.35 mm are recommended against vertebrate, aphid, lepidopteran and dipteran pests (Ester *et al.*, 1994). In the last decades, the cabbage whitefly (*Aleyrodes proletella*) has become an increasing pest problem in *Brassica* vegetables (Nebreda *et al.*, 2005). Recently, nets with 0.8 mm mesh size are recommended against cabbage whitefly (Saucke & Giessmann, 2003; Saucke *et al.*, 2004). However, cabbage whiteflies can still transit 0.8 mm nets (Lessing, 2013) and several farmers expressed doubt on their efficacy (pers. com.). During previous field studies, we additionally observed lower whitefly numbers on Brussels sprouts under fine meshed nets compared to unprotected Brussels sprout plants early in the cropping season, but also high whitefly numbers under fine meshed nets in the late cropping season. In sum, there is need for a comprehensive comparison of the effect of crop cover nets with different mesh sizes on whitefly abundance, thereby also considering other pests of Brussels sprouts as well as natural enemies.

The cabbage whitefly is oligophagous, feeding on several plant species of the family Brassicaceae but also on other families (see Evans, 2007 for a list of host species). Since the cabbage whitefly overwinters and reproduces in oilseed rape, areas with high oilseed rape farming suffer from severe damage (Belder *et al.*, 2008; Ludwig *et al.*, 2014; Richter & Hirthe, 2014b). Overwintering whitefly females start laying eggs on oilseed rape in April, and adults of the first generation appear in June (Richter & Hirthe, 2014b). Those adults disperse to find new host plants in June and July when oilseed rape fields dry during ripening (Ludwig *et al.*, 2014; Richter & Hirthe, 2014b). Dispersing whiteflies are reported to fly for 0.5 to 1 km (Bährmann, 2002).

Besides whiteflies, also cabbage aphid (*Brevicoryne brassicae*), peach-potato aphid (*Myzus persicae*) and diamondback moth (*Plutella xylostella*) are important *Brassica* pests and frequently found on Brussels sprout. Under the temperate climate conditions in the study region, both aphid species hibernate predominantly as eggs, cabbage aphids on host plants of the family Brassicaceae (such as winter oilseed rape, overwintering cabbages or wild *Brassicas*) and peach-potato aphids on *Prunus sp*. (Capinera, 2001). After the hatching of the fundatrices in spring, they bear a new generation on of potential colonisers of new host plants. In April (peach-potato aphid), respectively, May (cabbage aphid), first winged individuals can be found on the new host plants such as vegetable *Brassicas* (Kirk, 1992). While cabbage aphids almost exclusively colonise Brassicaceae, the peach-potato aphid has a very broad host range (Capinera, 2001). Overwintering of the diamondback moth under temperate climate conditions is not conclusively clarified. It may either be migratory or hibernate locally (Jacobs *et al.*, 1998; Furlong *et al.*, 2013). However, first adults are observed in May in central Europe (Jacobs *et al.*, 1998). The caterpillars feed on plants of the family of Brassicaceae only (Capinera, 2001).

As nets can also hinder colonisation by natural enemies (Hommes, 1993), we were also interested in aphid parasitism as well as presence of predators such as hoverfly larvae and spiders. The parasitic wasp *Diaeretialla rapae* is an important parasitoid of cabbage aphid and peach-potato aphid, reducing population growth of both species (Hafez, 1961; Pike *et al.*, 1999; Desneux *et al.*, 2005; Neuville *et al.*, 2016). *D. rapae* hibernates inside mummies. It hatches and colonises aphid colonies from April onwards (Hafez, 1961). Syrphid larvae are another important natural enemy of aphids (Tenhumberg & Poehling, 1995). They also feed on whiteflies and small caterpillars (Dempster, 1967; Rijn *et al.*, 2008). The most abundant syrphid species in fields of vegetable *Brassicas* in the study region is *Episyrphus balteatus* (Hafez, 1961). This species is partly migratory and partly overwinters locally (Hondelmann &

Poehling, 2007). Its eggs can be found from end of March on winter host plants of aphids (Zwölfer *et al.*, 1984; Schier, 1988), while the second generation starts to colonise summer hosts of aphids late May (Tenhumberg & Poehling, 1995). Also spiders can affect aphid populations seriously (Wyss *et al.*, 1995; Schmidt *et al.*, 2003; Monzó *et al.*, 2009). In Brussels sprout fields as well as in other agricultural area Linyphiidae are often the most abundant spider family (Schmidt *et al.*, 2003; Geiger *et al.*, 2009). Linyphiid spiders frequently overwinter in grassy field margins (Geiger *et al.*, 2009).

To address the suitability of crop covers regarding whiteflies, other *Brassica* pest species and important natural enemies, we compared the impact of nets with different mesh size on infestation of Brussels sprouts by pests and their antagonists in a field study. Additionally, the amount of oilseed rape growing in the surrounding landscape was considered. We hypothesise that: 1. The abundance of pests and natural enemies on Brussels sprouts decreases with decreasing net mesh size. 2. The effect of nets reducing pest and natural enemy numbers decreases during the growing season. 3. Infestation by pests predominantly specialised to the family Brassicaceae (i.e. cabbage whitefly, cabbage aphid and diamondback moth) increases with increasing amount of oilseed rape in the surroundings of Brussels sprout fields.

2. Materials and methods

The study was carried out on eleven organic horticultural farms in north-western Germany in 2014. All farmers grew a wide variety of vegetables including Brussels sprouts (*Brassica oleracea* var. *gemmifera*) and other cole crops (*Brassica oleracea* varieties). They planted Brussels sprouts between late April and late May and harvested for the first time in late October or November. In mild winters harvesting continues until spring and the remaining parts of the pants are ploughed under between February and March, one to two months before new cole crops are planted. Farmers covered newly planted cole crops either with fine (0.8 mm) or intermediate (1.35 mm) mesh size nets (see Appendix C Table C.1). To investigate effects of net mesh size, two control plots with ten plants each were considered per farm. Control plots were initially covered by the farmer’s fine / intermediate mesh size nets, which we changed against wide (7 mm) mesh nets about 3 weeks after planting to protect plants from vertebrate pests but allow access to the crop by most arthropods. The survey took place in June (the time of summer migration of the cabbage whitefly (Richter and Hirthe 2014)), in August and in October (shortly before harvest). We recorded the presence of pest insects (whiteflies, aphids and all kinds of caterpillars) and their natural enemies (syrphid eggs, larvae and pupae, all kinds of spiders, lady beetles, common lacewings, earwigs and aphid mummies) on 12 plants per farm under fine or intermediate meshed nets and on 20 plants per farm under the 7 mm nets (plant numbers sampled under different net types differ because data were initially collected for two different studies). Whitefly parasitism was not recorded. As long as plants were small (≤ 15 leaves) insects on all leaves were recorded. When plants had > 15 leaves, we checked ten randomly selected leaves per plant covering different leaf ages. In case of heavy infestation by one or more developmental stages of the cabbage whitefly (egg clutches, larvae or adults), this developmental stage was only recorded on six plants per farm and net treatment. Heavy infestation was defined as > 50 individuals of a developmental stage on each of the first six plants sampled. We mapped oilseed rape fields in a 1 km radius around all farms.

2.1. Analysis of data

Data were excluded from statistical analysis if nets were removed by farmers before the end of the study or if nets of 1.35 mm mesh size were used, which were too rarely used in recent years on sampled farms for a statistically sound analysis (for data including all fields and mesh sizes with indications of net removal, see Appendix C Table C.1 and Fig. C.1 – C.2). To investigate the impact of net mesh size and the amount of oilseed rape in the surrounding landscape within the three sampling periods (June, August and October) we calculated the mean number of individuals of each pest or natural enemy group per leaf for each sampling period, net type and farm. These dependent variables were log-transformed to account for non-normality in count data. Aphid parasitism rates were not transformed. As explanatory variables we used: net mesh size (0.8 vs. 7 mm) and sampling period (June vs. August vs. October) as categorical variables. For pest species, the oilseed rape area in a 1 km radius was added as additional explanatory variable. Further, all two-way interactions were included. For natural enemies, the mean availability of prey (sum of aphids, whitefly egg clutches, larvae and adults), respectively, hosts (aphids) per leaf for each sampling period, net type and farm was calculated and included as covariable. The analysis of aphid parasitism was done with data from August and October only, because hosts were observed in June on a few farms only. The data were analysed using linear mixed effects models to account for repeated sampling at each study site (random effect = farm). Models were simplified by calculating the second-order Akaike information criterion (AICc, appropriate for small sample sizes) for all full model subsets using the dredge function in the muMIn (multi-model inference) package (Burnham & Anderson, 2002; Barton, 2015). Variables remaining in the model with the lowest AICc are discussed. All calculations were run with R version 3.3.0 (R Core Team, 2016). R^2 values were calculated using the sem.model.fits function from the piecewiseSEM package version 1.1.2 (Lefcheck, 2015). We report marginal R^2 (marg. R^2) values corresponding to the proportion of variance explained by fixed factor(s) alone and conditional R^2 (cond. R^2) corresponding to the proportion of variance explained by fixed and random factors (Nakagawa & Schielzeth, 2013).

3. Results

Pests counted on 4965 leafs of 500 sampled plants were included in the analyses (310 ± 23 leaves were sampled per farm and sampling date, mean ± SD). The cabbage whitefly was the most important pest with a median density of 175 egg clutches, 605 larvae and 160 adults per 100 leaves. The second most abundant pest was the peach-potato aphid (median of 23 individuals per 100 leaves) followed by the cabbage aphid (median of 17 individuals per 100 leaves) and the diamondback moth (median of 0.5 caterpillars and 0.3 pupae per 100 leaves). Aphid parasitism ranged between 0.5 and 37 % (median of 17 %). The most frequent predators were spiders (median of 5 individuals per 100 leaves) followed by syrphids (median of 0.3 eggs, 0.3 larvae and 0 pupae per 100 leaves). While the cabbage whitefly and both aphids showed the highest densities in October, diamondback moth and natural enemies were most abundant in August (Table 3.1).

Table 3.1 Median, maximum and minimum abundances of the investigated taxa per 100 leaves per farm for each sampling month.

	June			**August**			**October**		
	Median	**Max**	**Min**	**Median**	**Max**	**Min**	**Median**	**Max**	**Min**
Cabbage whitefly	158	3685	22	2545	19115	830	9186	22532	691
Egg clutches	114	2324	13	592	5045	69	0	19	0
Larvae	0	844	0	1194	10887	509	5479	18838	501
Adults	50	530	9	398	3183	60	3675	3707	191
Cabbage aphid	2	35	0	26	992	9	85	650	13
Peach-potato aphid	1	61	0	56	2421	4	461	864	25
Diamondback moth	0	4	0	21	90	1	0	3	0
Caterpillars	0	3	0	12	76	0	0	1	0
Pupae	0	1	0	10	14	1	0	2	0
Aphid parasitism [%]	5	10	1	20	37	14	5	25	1
Syrphids	0	9	0	13	35	3	0	1	0
Eggs	0	6	0	7	20	1	0	0	0
Larvae	0	3	0	6	13	1	0	1	0
Pupae	0	0	0	1	2	0	0	0	0
Spiders	3	4	0	13	29	5	7	14	4

The model with the lowest AICc for the cabbage whitefly contained effects of net mesh size ($p < 0.001$), sampling period ($p < 0.001$), a positive effect of oilseed rape area in a 1 km radius area around the study sites ($p = 0.076$), an interaction between sampling period and oilseed rape area ($p = 0.001$) as well as an interaction between sampling period and net mesh size ($p = 0.036$; model's marg. $R^2 = 0.75$, cond. $R^2 = 0.90$). The interaction between sampling period and oilseed rape area shows that the number of whiteflies increased only slightly with oilseed rape area in June, while the slope was steeper in August and steepest in October (Fig. 3.2a). The interaction between sampling period and net mesh size showed that the difference between 0.8 mm and 7 mm nets was visible as a trend in June, most pronounced in August, but disappeared in October (Fig. 3.1a, Fig. 3.2b). For the cabbage aphid, the null model showed the lowest AICc. For the peach-potato aphid net mesh size ($p = 0.026$), sampling period ($p = 0.081$) and an interaction between sampling period and net mesh size ($p = 0.034$) remained in the best model (model's marg. $R^2 = 0.36$, cond. $R^2 = 0.42$). Peach-potato aphid density was generally low in June and increased with time under 0.8 mm nets, while no change in peach-potato aphid numbers occurred under 7 mm nets (Fig. 3.1c, Fig. 3.2c). For the diamondback moth, the best model showed an effect of sampling period ($p = 0.029$; model's marg. $R^2 = 0.21$, cond. $R^2 = 0.22$) with increasing abundance during the growing season (Fig. 3.1d).

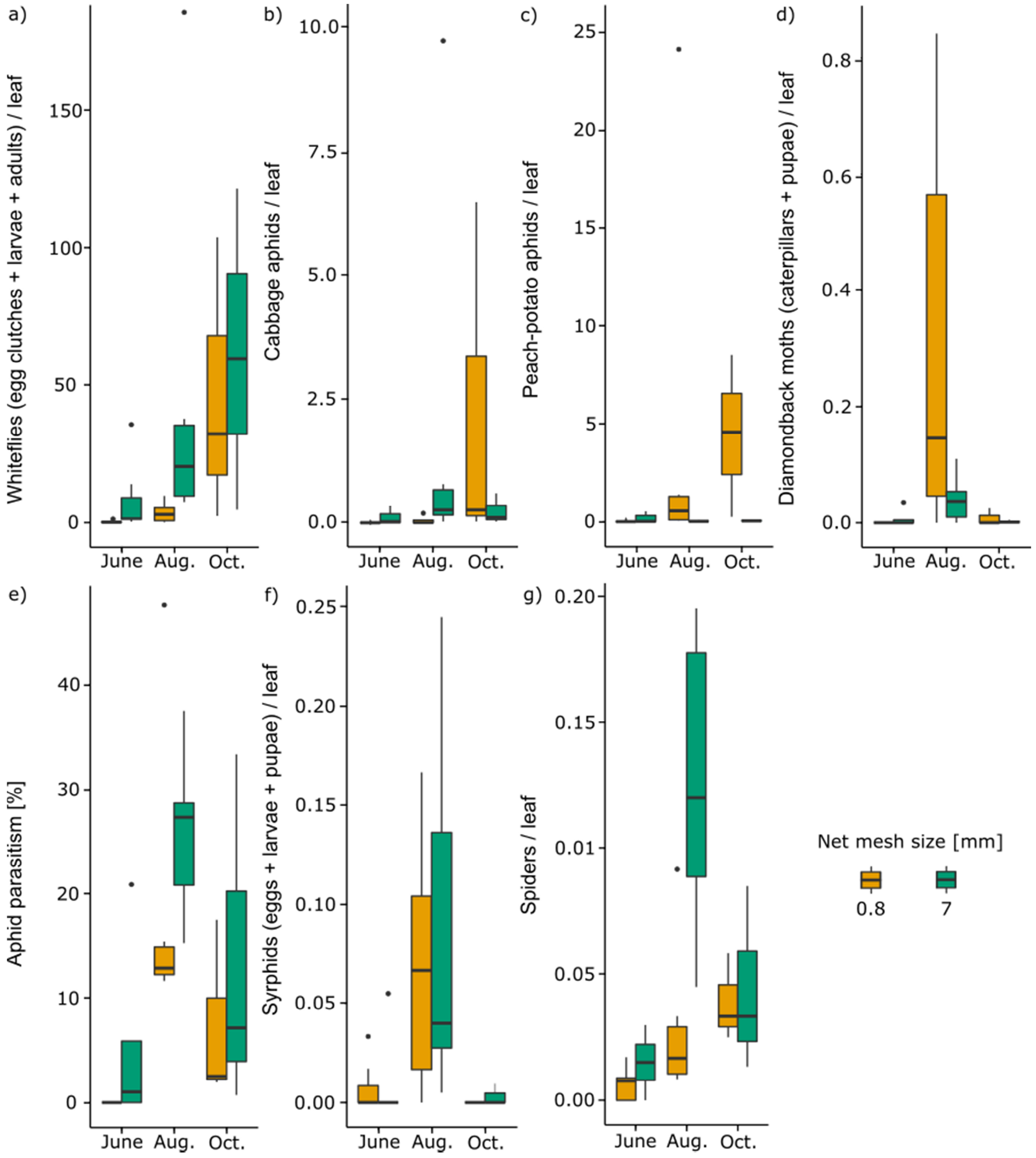

Fig. 3.1 Population development of different pest insects and natural enemies on Brussels sprouts under nets of 0.8, 1.35 and 7 mm mesh size in June, August and October: a) cabbage whitefly, b) cabbage aphid, c) peach-potato aphid, d) diamondback moth, e) aphid parasitism f) syrphid eggs, larvae and pupae, g) spiders.

For the aphid parasitism rate, the null model showed the lowest AICc, but a trend towards higher parasitism under 7 mm nets compared to 0.8 mm nets is visible in Fig. 3.1e. For syrphids, the sampling period (p = 0.001) and a positive effect of prey availability (p = 0.039) remained in the model with the lowest AICc (marg. $R^2 = 0.43$, cond. $R^2 = 0.43$). Syrphid presence increased during the season (Fig. 3.1f). Spiders on Brussels sprout plants were affected by net mesh size ($p < 0.001$), sampling period ($p < 0.001$), prey availability ($p < 0.001$) and an interaction between sampling period and net mesh size ($p = 0.001$; model's marg. $R^2 = 0.76$, cond. $R^2 = 0.81$). The interaction clearly shows that higher spider densities were found under 7 mm nets compared to 0.8 mm nets in August, while spider numbers were generally low in June and October (Fig. 3.1g, Fig. 3.2d).

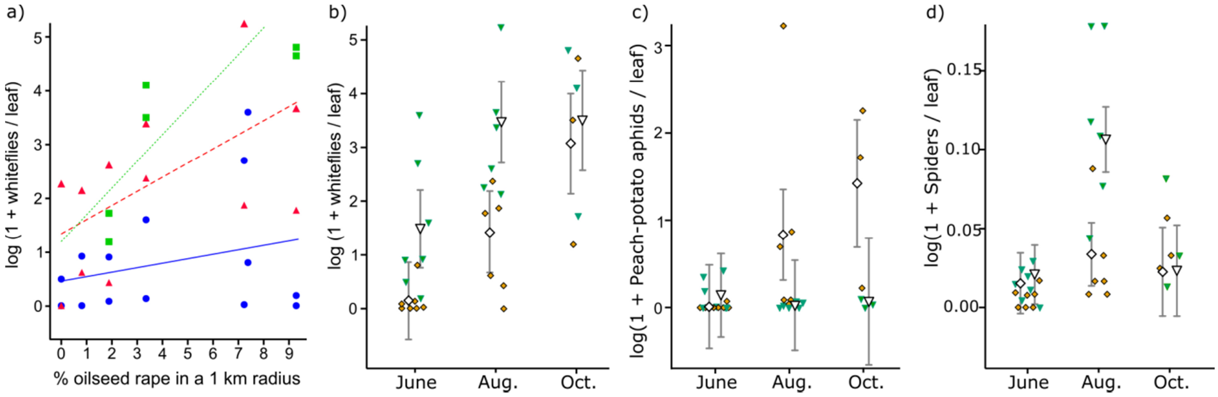

Fig. 3.2 Interacting effects of a) sampling period and oilseed rape area in a 1 km radius around study sites on whitefly densities. Data points and model predictions: June: dots and continuous line, August: triangles and dashed line, October squares and dotted line. Interacting effects of sampling period and net mesh size on b) whitefly c) peach-potato aphid and d) spider densities. Data points are horizontally jittered. Diamonds indicate 0.8 mm nets, triangles 7 mm nets. Filled small symbols are data points, large empty symbols are model predictions with 95 % confidence intervals.

4. Discussion

Effects of net mesh size on abundance of pests and natural enemies varied considerably between species and sampling periods. We hypothesised that the abundance of pests and natural enemies is the smaller the finer the net mesh size is, which was confirmed for the cabbage whitefly and for spiders. Also aphid parasitism tended to be lower under fine meshed nets. Thus, fine meshed nets seem to affect the colonisation of Brussels sprouts by both, pest species and natural enemies. The difference in whitefly and spider abundance under 0.8 mm and 7 mm nets was most pronounced in August but could not be detected in October. This is in accordance with our second hypothesis, stating that the effect of nets decreases during the growing season. Different reasons may cause this pattern. The first reason concerns the net mesh size: As 0.8 mm nets are an obstacle to cabbage whiteflies but can be crossed (Lessing, 2013), more and more whiteflies may cross the nets with passing time and start to reproduce under the net. Secondly, pests and natural enemies can find their way under nets through holes in damaged nets, during net removal for weeding or because some farmers did not take enough care to keep their nets as close as possible, e.g. nets were lifted from the ground by growing plants, building gateways for colonisation. Also the frequency and duration of net removal for weeding may have been handled differently by farmers.

In contrast to findings of Ester *et al.* (1994) some pests and antagonists were not affected by nets (cabbage aphid, diamondback moth, syrphids). The number of individuals of these insects colonising the crop was generally low in June, and therefore small differences between net types may not have been recognised. The peach-potato aphid showed even higher abundances under the fine 0.8 mm nets than under wider nets in October. A favoured microclimate or lower numbers of natural enemies (e.g. spiders) may have led to higher population build-up. Spiders can effectively reduce aphid populations (Wyss *et al.*, 1995; Monzó *et al.*, 2009). Therefore, some pests may develop high densities on plants protected by fine meshed nets (Hommes, 1993), as observed here for the peach-potato aphid.

The third hypothesis stated that abundance of pests specialised to the Brassicaceae will increase with increasing amount of oilseed rape in the surrounding landscape. This was only found for the cabbage whitefly and supports that oilseed rape is an important overwintering and early summer reproduction habitat for the cabbage whitefly (Belder *et al.*, 2008; Ludwig *et al.*, 2014; Richter & Hirthe, 2014b). While whitefly numbers increased only slightly with increasing oilseed rape area in June, the slope of the oilseed rape effect on cabbage whitefly abundance increased with time (Fig. 3.2a). Previous analyses indicated that this interaction was mainly caused by whitefly abundances under 0.8 mm nets. Especially in June and August the effect of oilseed rape area seemed to be stronger on plants covered by 7 mm nets than on those covered by 0.8 mm nets, which hinder colonisation.

The other pest species appeared in considerably lower densities than the cabbage whitefly which may hamper the detection of a relation between their numbers on Brussels sprouts and oilseed rape as a source habitat. Additionally, the location of source habitats in relation to prevailing wind directions may be important for wind dispersed species such as aphids or whiteflies, as those insects are mainly transported from upwind source habitats towards the study sites (Byrne *et al.*, 1996; Compton, 2002). Additionally, interference with barriers such as hills, forests or hedges affects wind dispersal (Pasek, 1988). Therefore, the incorporation of prevailing wind directions and presence of relevant landscape elements into analyses could have led to (more) distinct pattern. However, cabbage aphids were rarely found in winter oilseed rape fields in the study region (chapter 1). This reduces the probability of oilseed rape fields being source habitats for cabbage aphids – although they are sometimes found to overwinter in large numbers in oilseed rape fields (Hafez, 1961; Collier & Finch, 2007).

The peach-potato aphid is probably affected by different habitats, because it is a generalist species that feeds on several plant species of which at least pumpkin, potato and corn were present on the horticultural farms of the current study. It hibernates on *Prunus sp.* trees in the egg stage but may also overwinter on plants in (green-) houses with temperatures > 4°C (Capinera, 2001). Also the diamondback moth shows no strong relation to oilseed rape in central Europe, in contrast to other parts of the world (Williams, 2010). One reason may be that it is a migratory species in temperate regions that reaches the study region not before May (Jacobs *et al.*, 1998; Furlong *et al.*, 2013) . Therefore the diamondback moth does not profit from high availability of oilseed rape fields as hibernation or early year reproduction habitats.

In conclusion, 0.8 mm nets can minimise the colonisation of *Brassica* vegetables by the cabbage whitefly and therefore are recommended in landscapes with high colonisation pressure by cabbage whiteflies, e.g. landscapes with high amount of oilseed rape. The use of 0.8 mm nets in practice has to be optimised to extend their effect to the end of the cropping period. We suggest minimising net removal during periods of high dispersal activity of pests, i.e. for cabbage whiteflies between midday and afternoon at days with warm and sunny weather conditions. Instead, net removal on cloudy days or during cool morning conditions may reduce colonisation by whiteflies (Stein, 1958). Additionally, the release of natural enemies under nets could help to increase the efficacy of nets, although this technic needs further development (Saucke *et al.*, 2011). Because 0.8 mm nets had negative effects on the presence of spiders, did not affect cabbage aphid and diamondback moth but even promoted peach-potato aphid, we recommend using wider nets in landscapes with low colonisation pressure by cabbage whiteflies.

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Chapter 4

Landscape effects on colonisation by pests and natural enemies only partly persist under production situation in Brussels sprout fields - a three years study

Abstract

The occurrence of pests and natural enemies in agricultural crops is related to colonisation from the surrounding landscape. Effects of different landscape elements (mainly area of oilseed rape and arable land or permanent habitats) on colonisation of young Brussels sprout plants by pests and natural enemies were investigated in chapters 1 and 2. These landscape effects on colonisation can, but not necessarily need to, affect later pest densities and crop damage. This chapter investigates how landscape elements with potential relevance for crop colonisation affect pest pressure in Brussels sprout fields during the cropping season. We counted arthropods in Brussels sprout fields in three consecutive years and recorded the surrounding landscapes as well as prevailing wind directions for each field. The most abundant pests were cabbage whiteflies followed by cabbage aphids, peach-potato aphids and diamondback moths; the most abundant natural enemies were syrphid larvae, spiders and aphid parasitoids (recorded as parasitism rate). Cabbage whitefly abundance was positively related to oilseed rape area throughout the year. Marginal and significant positive effects by arable land area were shown for cabbage aphids and spiders in midsummer, respectively. No further landscape effects on abundances of the named species were found, and no increased model quality due to weighting of habitats by prevailing wind directions could be detected. Thus, some effects of importance for colonisation detected in chapter 1 did not persist under crop production situation in Brussels sprout fields, possibly due to additional variability caused by differences in management practices, population development or data inclusion from three years. The example of the effect of oilseed rape area on the cabbage whitefly showed that landscape effects on colonisation in early summer can determine pest densities even shortly before harvest. Therefore the need for crop protection and the cost effectiveness can be directly related to the area of oilseed rape in the surrounding landscape for the production of *Brassica* vegetables which are sensitive to damage by the cabbage whitefly.

1. Introduction

The occurrence of most organisms in their habitats, such as arthropods in crop fields, is related to the surrounding landscape (Andrén, 1994; Tscharntke *et al.*, 2005). Especially in agricultural landscapes, which are characterised by periodic and abrupt changes in habitat quality and availability, crop fields are frequently recolonised from the surroundings (Wissinger, 1997). Sources for recolonisation by many arthropod species, among them pests and their natural enemies, can be semi-natural habitats such as extensively used grasslands, field margins or waysides but also other crop fields (Blitzer *et al.*, 2012; Riedinger *et al.*, 2014). Sustainable crop protection concepts such as integrated or organic farming need a detailed knowledge on which habitats affect the presence of pests and natural enemies. They need to consider time and scale of this mostly species-specific relationship (Naranjo *et al.*, 2010; Dinsdale *et al.*, 2012).

Winter oilseed rape fields are source habitats for colonisation of vegetable *Brassicas* by pests, which are often specialised to plants of the family of Brassicaceae (chapters 1, 2 and 3, Richter & Hirthe, 2014b). Additionally, several studies showed that landscape complexity, which is often measured as area of arable land, negatively affects the occurrence of in particular predatory and parasitoid species (Roschewitz *et al.*, 2005; Haenke *et al.*, 2009; Meyer *et al.*, 2009). Landscapes with high complexity often offer a high proportion of permanent, extensively used habitats (Vollhardt *et al.*, 2008). These permanent (often called 'semi-natural') habitats are important source habitats for colonisation of crop fields by many arthropods, but special attention has been payed to their importance for natural enemies of pests (Blitzer *et al.*, 2012). Field margins and waysides, for example, are important overwintering habitats for spiders and other natural enemies; therefore they can support colonisation of crop fields and control of pests (Geiger *et al.*, 2009). Also grasslands can serve as source habitats as they have many spider species in common with arable fields and harbour higher densities (Schmidt & Tscharntke, 2005). In contrast, the abundance of aphidophagous syrphids was shown to increase in landscapes with high proportion of arable land, which effectively support their larvae with prey (Haenke *et al.*, 2009; Meyer *et al.*, 2009).

The importance of source habitats for a patch that is colonised (e.g. a crop field) can vary depending on their relative location to the colonised patch. Source habitats in an up-wind direction from the colonised patch can be of high importance, as the dispersal of several small arthropods such as aphids, whiteflies or ballooning spiders is characterised by wind transport (Compton, 2002, chapters 1 and 2). On the other hand, several insects such as moths or syrphids locate food by following olfactory cues in an upwind flight (Palaniswamy *et al.*, 1986; Budenberg & Powell, 1992, chapters 1 and 2). Consequently, source habitats in down-wind direction from the colonised patch are of highest importance for colonisation by those olfactory orientated insects (Moser *et al.*, 2009).

Previous chapters show increasing colonisation of young Brussels sprout plants by cabbage whiteflies (*Aleyrodes protelella*) and cabbage aphids (*Brevicoryne brassicae*) in early summer with increasing oilseed rape area in the surrounding landscape (chapters 1 and 2). Thereby upwind oilseed rape area was of increased importance for colonisation by cabbage whiteflies (passive wind transport) while downwind oilseed rape area was of increased importance for cabbage aphids (possibly due to olfactory orientated upwind flight). In contrast, colonisation of young Brussels sprout plants by the diamondback moth (*Plutella xylostella*) was not affected by oilseed rape area but tended to be higher in landscapes with higher landscape complexity (lower area of arable land) when additional weight was given to downwind located habitats (chapter 1).

In chapters 1 and 2 colonisation of the named species was investigated in early summer using standardised monitoring plants. In contrast to samplings of plants of Brussels sprout fields, data from monitoring plants are a snapshot, focussing on immigration and minimising additional variability due to different management practices that affect reproduction, mortality and emigration. Colonisation intensity is of great importance for crop damage forecasts as it lays the foundation for future pest populations in crop fields. However, not colonisation itself but a potentially following high pest infestation, built up during the growing season, is the direct cause of crop damage. This final chapter investigates to what extend results on the factors that drive colonisation of monitoring plants can be transferred into crop production situation in Brussels sprout fields. Thereby it not only refers to the early summer, the time of colonisation peak of most cabbage pests, but also to later dates of the cropping season when pest infestation is highest. Thus we investigated pests' and natural enemies' abundances on plants of Brussels sprout fields at different times of the year. Since the importance of different colonisation sources can vary between years (Vialatte *et al.*, 2007), a high generality and transferability of our results was ensured by including data from three years. Furthermore, additional landscape characteristics with potential effects on the presence of natural enemies were considered.

1.1. Research questions and hypotheses

1. Are the abundances of different pest species (cabbage whitefly, cabbage aphid, peach-potato aphid (*Myzus persicae*), diamondback moth) affected by oilseed rape area or landscape complexity (area of arable land) in the surrounding landscape?

   We thereby hypothesise, based on the results of the first chapter, that the abundances of cabbage whitefly and cabbage aphid are positively affected by oilseed rape area, while the diamondback moth is positively affected by landscape complexity (i.e. negatively by the area of arable land).

2. Are the abundances of syrphid larvae and spiders as well as aphid parasitism rates affected by landscape complexity (area of arable land), the area of waysides or grasslands in the surrounding landscape in addition to prey/host availability?

   We hypothesise, following the results of the first chapter, that landscape complexity does not affect syrphid abundance in addition to a positive effect of prey availability.

3. Are the detected landscape effects strengthened by giving additional weight to upwind or downwind landscape?

   We hypothesise in accordance to the results of the first chapter, that the landscape effect on cabbage whitefly is strongest when additional weight is given to upwind landscape (indicating wind dispersal) and the landscape effects on cabbage aphid and diamondback moth are strongest when additional weight is given to downwind landscape (indicating olfactory orientation in upwind flights).

4. Do the detected landscape effects change throughout the growing season?

2. Materials and methods

2.1. Field work

Data on abundances of pests and natural enemies originated from samplings in organic Brussels sprout fields in north-western Germany in three consecutive years (11 to 16 fields per year). Each field was sampled once during three sampling periods named ‘June/July’ (6th of June to 12th of July), ‘July/August’ (29th of July to 22th of August) and ’October’ (1st to 24th of October). Sampled plants were selected at random distances between one and five meters along a transect through the field. The number of sampled plants and the number of sampled leaves per plant differed among years (as data originated from studies with different key issues in the different years) and among sampling periods (as the sampling effort was reduced in the later sampling periods to hold similar survey time periods when plants size and arthropod abundances increased; see Appendix D Table D.1). We accounted for these differences in sampling methodology by calculating mean arthropod abundances per 100 leaves for each farm and year. All farms used nets as crop protection measure; most nets had a mesh size of either 0.8 or 1.35 mm. As some farms used insecticides, only data from samplings before insecticide treatments at those farms were included.

2.2. Land use and wind

Land use was mapped in 1 km radii around study fields in each of the three years. We grouped land use by the categories oilseed rape, arable land and grassland. The percentage land cover of these land use categories was calculated in the 1 km radii around study fields. Further, the percentage area of waysides in 1 km radii around study fields was estimated by taking roads and tracks outside settlement areas from ATKIS maps (Official Topographic-Cartographic Information System, Germany) and assuming a mean wayside width of 0.5 m on both sides of each road or track. The percentage of wayside area in 1 km radius landscapes per study field and year was calculated. Weather stations were placed to record wind directions on all study fields and in every year. Wind data were used to weight the landscape variables, once by giving additional weight to upwind located habitats (to account for passive wind dispersal, hereafter named ‘upwind weighted’ habitats) and once by giving additional weight to downwind located habitats (to account for upwind oriented host finding, hereafter named ‘downwind weighted’ habitats). The weighting was processed as described in chapters 1 and 2, but instead of only using separate wind data for day and night time recorded 2 weeks before sampling we used 24 h wind data recorded from June to October of the relevant years.

The distribution of prevailing wind directions of this period in time was similar compared to the 2 week recordings used in chapters 1 and 2 (see Appendix D Fig. D.1).

2.3. Statistics

The statistical analysis was done in R (version 3.3.2., R Core Team, 2016). Mean abundances of the following taxa were calculated per 100 leaves for each farm and year (field) as response variables: cabbage whiteflies (egg clutches, larvae, adults and sum of these developmental stages), cabbage aphids, peach-potato aphids, diamondback moths (sum of caterpillars and pupae), syrphids (sum of eggs, larvae and pupae) and spiders. These data were log-transformed to account for non-normality of count data. Aphid parasitism rates were calculated as number of mummies divided by the total number of aphids (including mummies). The aphid parasitism rate was logit-transformed.

Since landscape in an 1 km radius around study fields explained colonisation best in chapter 1, the percentage areas of oilseed rape and arable land in an 1 km radius were used as explanatory variables regarding pest species. Regarding predators (syrphids, spiders) and aphid parasitism rates, we additionally used the percentage areas of waysides and grasslands as explanatory variables and always added prey or host availability as covariable. Testing for oilseed rape amount was omitted due to its strong correlation with prey or host availability. In addition, these maximum models contained two further covariables: the day of the sampling period (to account for population growth during sampling periods) and a variable coding for mesh size (in June/July and July/August) or presence of nets (in October). Explanatory variables and covariables were log-transformed whenever necessary to lower the importance of extreme values (oilseed rape area, grassland area, number of prey and host insects). The absolute values of Spearman's correlation coefficients among included explanatory variables were always below 0.6 and variance inflation factors in a linear model were always below three ($|r| \leq 0.6$, $VIF \leq 3$; Zuur *et al.*, 2010; Dormann *et al.*, 2013). Variance inflation factors are a measure for how much of an explanatory variable's variation is explained by the other explanatory variables of a model (Zuur *et al.*, 2010).

Linear mixed-effects models were used to account for repeated sampling on the same farm's fields during the three years (package: lmerTest, version 2.0-32, Kuznetsova *et al.*, 2016). Additionally to the named maximum models, we calculated models testing each of the maximum models' explanatory variables separately. In the next step, models for all possible combinations of variables with at least marginal significant effects ($p < 0.1$) were calculated. All models were ranked for each investigated taxon according to the second-order Akaike information criterion appropriate for small sample sizes (AICc) (Burnham & Anderson, 2002). If the best models, i.e. the models in a $\Delta AICc = 2$ range, contained marginal significant or significant effects ($p < 0.1$) of landscape variables, we additionally calculated models including the relevant landscape variables once with upwind weighting and once with downwind weighting of habitats. Variables which showed an effect with $p < 0.1$ in models within the final $\Delta AICc = 2$ range were discussed.

3. Results

We sampled pests and their natural enemies on altogether 26,426 leaves belonging to 2,630 plants on 43 Brussels sprout fields within three years. The cabbage whitefly was the by far most numerous pest species. Due to its high abundance, its developmental stages could be analysed separately. Other important pests (cabbage aphid, peach-potato aphid, diamondback moth) were found less frequently and their developmental stages were pooled in the analysis. The most abundant natural enemies were syrphids, spiders and aphid parasitoids (recorded as parasitism rate). The population development of these most numerous pests and natural enemies is displayed in Fig. 4.1.

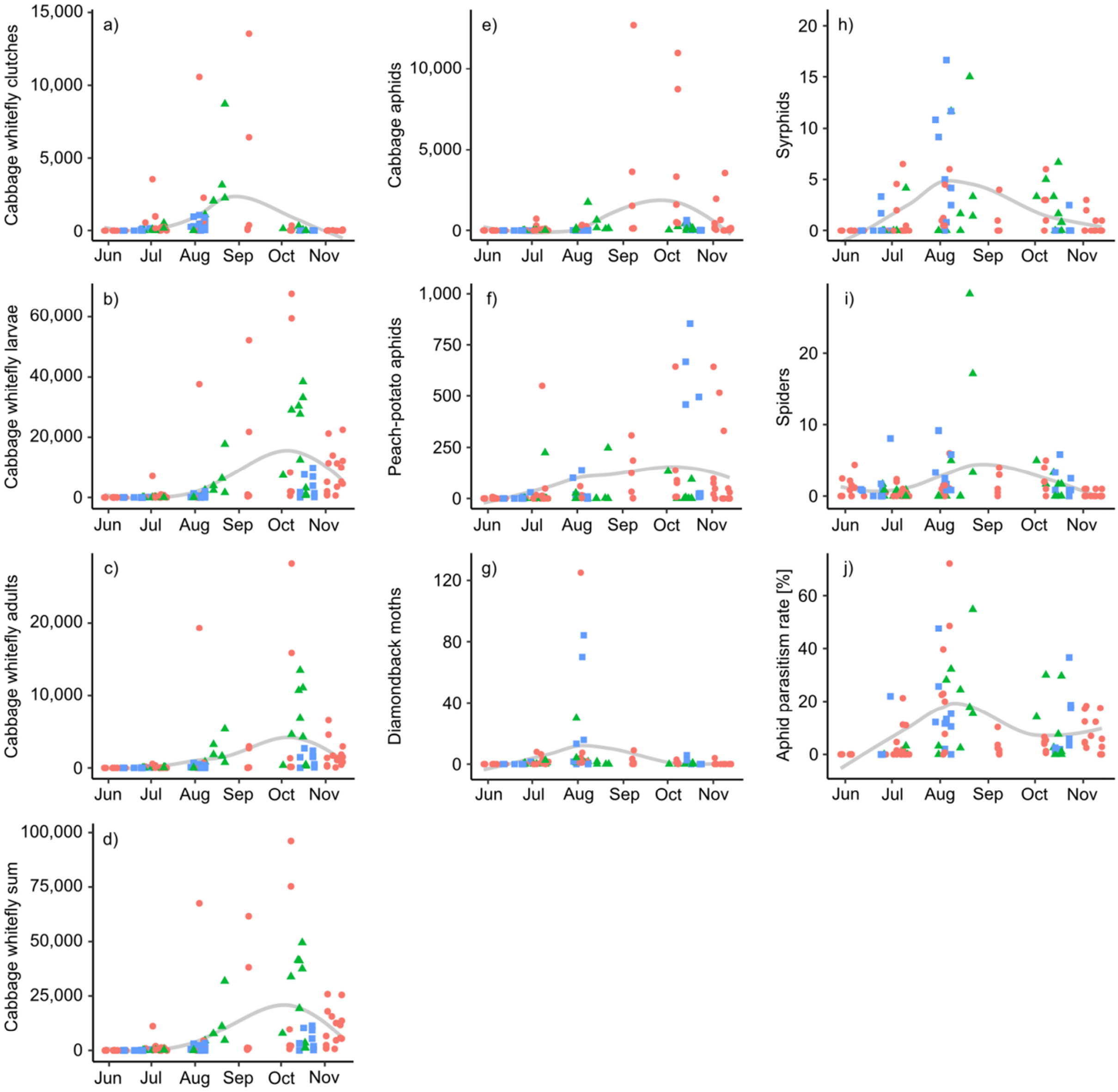

Fig. 4.1 Population development of the most numerous pests and natural enemies in Brussels sprout fields during the course of the year: cabbage whitefly a) egg clutches, b) larvae, c) adults, d) sum of all whitefly stages, e) cabbage aphids, f) peach-potato aphids, g) sum of diamondback moth caterpillars and pupae, h) sum of syrphid eggs, larvae and pupae, i) spiders and j) aphid parasitism rate. Displayed are also samplings from early June, September and November 2012, which were not part of the analyses. The figures show mean abundances per 100 leaves per field and sampling day in three consecutive years: red dots = 2012, green triangles = 2013, blue squares = 2014, grey lines = smoothed line showing the overall trend. Two outliers are not displayed: 2415 peach-potato aphids per 100 leaves, 05. August 2014 (f) and 43 immature syrphid stages per 100 leaves, 31. July 2014 (h).

Other pests and natural enemies were generally observed in low abundances within the three years, namely small whites (*Pieris rapae*: 130 eggs, 128 caterpillars, 19 pupae), large whites (*Pieris brassicae*: 116 caterpillars), cabbage moths (*Mamestra brassicae*: 82 caterpillars), Silver Ys (*Autographa gamma*: 17 caterpillars, 3 pupae), green lacewings (Chrysopidae: 11 eggs, 3 larvae, 1 pupa), lady beetles (Coccinellidae: 13 larvae, 7 pupae, 62 adults of which 52 were *Harmonia axyridis*). Although the named minor pests generally occurred in low abundances, some reached high densities on single farms and caused severe damage.

Statistical analyses of different developmental stages of the cabbage whitefly showed similar results (Tables 4.1 and 4.2). Abundances of all developmental stages of each sampling period could be analysed except for larval abundance in June/July and egg clutch abundance in October. All developmental stages of the cabbage whitefly were found more often in landscapes with a high percentage of oilseed rape in all three analysed sampling periods (p-values ranged from 0.020 to < 0.001). Even though upwind or downwind weighting of oilseed rape area in some cases showed lower p-values, the model without weighting by wind was always in the range of the best models (ΔAICc = 2). This indicates no significant differences between models with and without weighting of oilseed rape area by prevailing wind directions. Furthermore, the abundance of all developmental stages increased during the sampling periods June/July and July/August (lowest p-values = 0.003 and 0.025, respectively; Tables 4.1 and 4.2).

Cabbage aphid abundance could be analysed in July/August and October. It was marginally positively related to the area of arable land in July/August (lowest p-value = 0.066). Thereby models without weighting by wind were of better quality (lower AICc) than models with upwind or downwind weighting of area of arable land. Additionally, cabbage aphids were more abundant under nets with a wider mesh size in July/August (lowest p-value = 0.037). However, the similar quality of the null model (ΔAICc = 0.26) indicated weakness of both effects. Neither the investigated landscape variables nor net cover significantly affected cabbage aphid abundance in October, but cabbage aphid abundance significantly decreased during the sampling in October ($p = 0.019$).

Peach-potato aphid abundance could only be analysed in July/August. The null model was the only model in the ΔAICc = 2 range, and none of the tested variables had significant effects on peach-potato aphid abundance.

The diamondback moth abundance, analysed in July/August only, was not affected by any of the landscape variables. More diamondback moths were found under fine meshed than under wide meshed nets ($p = 0.052$), while their abundance decreased significantly during the sampling period (lowest p-value = 0.006; Tables 4.1 and 4.2).

Syrphid abundance, likewise analysed in July/August only, was related to none of the landscape variables. It significantly increased with increasing abundance of prey insects ($p = 0.017$).

Spider abundance was analysed in July/August and October. Its abundance increased with increasing area of arable land (lowest p-value = 0.036). Thereby models without weighting by wind explained spider abundance similarly well as models with upwind or downwind weighting of arable land. Spider abundance further increased during July/August (lowest p-value = 0.004). In October, spider abundance was not affected by any of the investigated landscape variables, but was higher on fields that were still covered by nets (lowest p-value = 0.007). Further, spider abundance significantly decreased during the sampling in October ($p = 0.080$).

The parasitism of aphids could be analysed in July/August and October, but was not significantly affected by any tested variable in both sampling periods. The lowest AICc was ascribed to the null model in both sampling periods.

Table 4.1 Best models according to the ΔAICc = 2 criterion for cabbage whiteflies (CW), cabbage aphids (CA), peach-potato aphids (PPA), diamondback moths (DMB), syrphids, spiders and aphid parasitism rates (Para. rate). Landscape variables of importance were: area of oilseed rape [%] (OSR), arable land [%] (AL) and area of waysides [%] (WS). Significant landscape variables within the best models were tested with downwind weighting of habitats (down) and with upwind weighting of habitats (up) in addition to their unweighted version. Models included the following covariables: day of the sampling period (day), mesh size of nets (net_mw), presence/absence of nets (net_pa) and prey abundance (prey). Estimates ± standard errors (Est. ± SE) and p-values are given. In some sampling periods abundances were too low for the analysis (x).

Taxon	Sampling period	No farms / fields	Landscape				Covariables			ΔAICc
			Land use	Wind	Est. ± SE	p	Name	Est. ± SE	p	
CW clutches	'June/July'	15 / 36	**OSR**	**-**	**1.048 ± 0.345**	**0.005**	**day**	**0.159 ± 0.048**	**0.005**	0.00
CW clutches	'June/July'	15 / 36	**OSR**	**down**	**0.908 ± 0.334**	**0.011**	**day**	**0.169 ± 0.047**	**0.003**	0.71
CW clutches	'June/July'	15 / 36	**OSR**	**up**	**1.023 ± 0.361**	**0.008**	**day**	**0.160 ± 0.048**	**0.006**	1.34
CW clutches	'July/Aug.'	14 / 26	**OSR**	**up**	**1.543 ± 0.300**	**< 0.001**	**day**	**0.132 ± 0.055**	**0.025**	0.00
CW clutches	'July/Aug.'	14 / 26	**OSR**	**-**	**1.523 ± 0.305**	**< 0.001**	**day**	**0.125 ± 0.057**	**0.038**	0.82
CW clutches	'July/Aug.'	14 / 26	**OSR**	**-**	**1.352 ± 0.303**	**< 0.001**	-	-	-	1.21
CW clutches	'October'	16 / 33	x	x	x	x	x	x	x	x
CW larvae	'June/July'	15 / 36	x	x	x	x	x	x	x	x
CW larvae	'July/Aug.'	14 / 26	**OSR**	**-**	**1.545 ± 0.438**	**0.002**	-	-	-	0.00
CW larvae	'July/Aug.'	14 / 26	**OSR**	**up**	**1.474 ± 0.451**	**0.004**	**day**	**0.164 ± 0.082**	**0.057**	0.45
CW larvae	'July/Aug.'	14 / 26	**OSR**	**-**	**1.422 ± 0.453**	**0.004**	day	0.125 ± 0.081	0.140	1.00
CW larvae	'July/Aug.'	14 / 26	**OSR**	**up**	**1.601 ± 0.458**	**0.002**	-	-	-	1.01
CW larvae	'October'	16 / 33	**OSR**	**up**	**1.370 ± 0.208**	**< 0.001**	-	-	-	0.00
CW larvae	'October'	16 / 33	**OSR**	**-**	**0.900 ± 0.225**	**< 0.001**	-	-	-	0.80
CW adults	'June/July'	15 / 36	**OSR**	**-**	**1.200 ± 0.261**	**< 0.001**	**day**	**0.077 ± 0.032**	**0.022**	0.00
CW adults	'June/July'	15 / 36	**OSR**	**up**	**1.190 ± 0.270**	**< 0.001**	**day**	**0.085 ± 0.033**	**0.014**	0.80
CW adults	'July/Aug.'	14 / 26	**OSR**	**up**	**1.632 ± 0.382**	**< 0.001**	**day**	**0.157 ± 0.071**	**0.036**	0.00
CW adults	'July/Aug.'	14 / 26	**OSR**	**-**	**1.203 ± 0.378**	**0.004**	-	-	-	0.92
CW adults	'July/Aug.'	14 / 26	**OSR**	**up**	**1.408 ± 0.403**	**0.002**	-	-	-	1.58
CW adults	'July/Aug.'	14 / 26	**OSR**	**-**	**1.232 ± 0.391**	**0.005**	day	0.107 ± 0.068	0.145	1.67
CW adults	'October'	16 / 33	**OSR**	**-**	**1.428 ± 0.217**	**< 0.001**	-	-	-	0.00
CW adults	'October'	16 / 33	**OSR**	**up**	**1.441 ± 0.225**	**< 0.001**	-	-	-	1.43
CW sum	'June/July'	15 / 36	**OSR**	**-**	**1.022 ± 0.362**	**0.009**	**day**	**0.169 ± 0.050**	**0.005**	0.00
CW sum	'June/July'	15 / 36	**OSR**	**down**	**0.867 ± 0.350**	**0.020**	**day**	**0.178 ± 0.049**	**0.003**	0.85
CW sum	'June/July'	15 / 36	**OSR**	**up**	**0.990 ± 0.379**	**0.014**	**day**	**0.171 ± 0.050**	**0.005**	1.23
CW sum	'July/Aug.'	14 / 26	**OSR**	**up**	**1.525 ± 0.363**	**< 0.001**	**day**	**0.157 ± 0.067**	**0.028**	0.00
CW sum	'July/Aug.'	14 / 26	**OSR**	**-**	**1.440 ± 0.367**	**< 0.001**	-	-	-	1.00
CW sum	'July/Aug.'	14 / 26	**OSR**	**-**	**1.426 ± 0.375**	**< 0.001**	**day**	**0.125 ± 0.069**	**0.084**	1.02
CW sum	'July/Aug.'	14 / 26	**OSR**	**up**	**1.571 ± 0.383**	**< 0.001**	-	-	-	1.85
CW sum	'October'	16 / 33	**OSR**	**up**	**1.362 ± 0.204**	**< 0.001**	-	-	-	0.00
CW sum	'October'	16 / 33	**OSR**	**-**	**0.882 ± 0.224**	**< 0.001**	-	-	-	0.56

Table 4.1 (continued):

Taxon	Sampling period	No farms / fields	Landscape				Covariables			ΔAICc
			Land use	Wind	Est. ± SE	p	Name	Est. ± SE	p	
CA	'June/July'	15 / 36	x	x	x	x	x	x	x	x
CA	'July/Aug.'	14 / 26	**AL**	**-**	**0.041 ± 0.020**	**0.066**	**net_mw**	**1.374 ± 0.621**	**0.037**	0.00
CA	'July/Aug.'	14 / 26	-	-	-	-	-	-	-	0.26
CA	'July/Aug.'	14 / 26	-	-	-	-	net_mw	1.080 ± 0.636	0.103	0.54
CA	'July/Aug.'	14 / 26	AL	-	0.029 ± 0.018	0.138	-	-	-	0.90
CA	'October'	16 / 33	-	-	-	-	**day**	**-0.163 ± 0.019**	**0.019**	0.00
PPA	'June/July'	15 / 36	x	x	x	x	x	x	x	x
PPA	'July/Aug.'	14 / 23	-	-	-	-	-	-	-	0.00
PPA	'October'	12 / 24	x	x	x	x	x	x	x	x
DBM	'June/July'	15 / 36	x	x	x	x	x	x	x	x
DBM	'July/Aug.'	14 / 23	-	-	-	-	**day**	**-0.098 ± 0.034**	**0.012**	0.00
							net_mw	**-0.689 ± 0.333**	**0.052**	
DBM	'July/Aug.'	14 / 23	-	-	-	-	**day**	**-0.117 ± 0.036**	**0.006**	0.78
DBM	'October'	12 / 24	x	x	x	x	x	x	x	x
syrphids	'June/July'	15 / 36	x	x	x	x	x	x	x	x
syrphids	'July/Aug.'	14 / 23	-	-	-	-	**prey**	**0.216 ± 0.083**	**0.017**	0.00
syrphids	'October'	12 / 24	x	x	x	x	x	x	x	x
spiders	'June/July'	15 / 36	x	x	x	x	x	x	x	x
spiders	'July/Aug.'	14 / 23	**AL**	**down**	**0.015 ± 0.007**	**0.036**	**day**	**0.075 ± 0.028**	**0.015**	0.00
spiders	'July/Aug.'	14 / 23	**AL**	**-**	**0.015 ± 0.007**	**0.044**	**day**	**0.079 ± 0.028**	**0.010**	0.38
spiders	'July/Aug.'	14 / 23	**AL**	**up**	**0.014 ± 0.007**	**0.052**	**day**	**0.082 ± 0.028**	**0.008**	0.64
spiders	'July/Aug.'	14 / 23	-	-	-	-	**day**	**0.095 ± 0.029**	**0.004**	1.48
spiders	'October'	12 / 24	-	-	-	-	**day**	**-0.042 ± 0.018**	**0.080**	0.00
							net_pa	**-0.702 ± 0.235**	**0.007**	
spiders	'October'	12 / 24	-	-	-	-	**net_pa**	**-0.705 ± 0.255**	**0.011**	0.46
Para. rate	'June/July'	15 / 36	x	x	x	x	x	x	x	x
Para. rate	'July/Aug.'	14 / 23	-	-	-	-	-	-	-	0.00
Para. rate	'July/Aug.'	14 / 23	-	-	-	-	day	0.056 ± 0.044	0.212	1.49
Para. rate	'July/Aug.'	14 / 23	WS	-	3.199 ± 2.739	0.255	-	-	-	1.78
Para. rate	'October'	12 / 24	-	-	-	-	-	-	-	0.00

4. Discussion

The strong positive effect of oilseed rape area on colonisation of monitoring plants by cabbage whitefly (chapter 1) persisted under crop production situation in Brussels sprout fields. Also the highly significant positive effect of prey abundance on colonisation of monitoring plants by syrphids could be transferred into crop production situation in Brussels sprout fields. However, the positive effects of oilseed rape and arable land area on colonisation by cabbage aphids and diamondback moths, respectively, as well as the effects of prevailing wind directions found in chapter 1 did not persist under crop production situation in Brussels sprout fields. This nullification of effects might be ascribed to different population development within the Brussels sprout fields or to additional variability due to different management practices and inclusion of data from three years. The consideration of pests' and natural enemies' abundances on plants of Brussels sprout fields at different times of the year showed the seasonal persistence of the positive effect of oilseed rape amount on cabbage whiteflies as well as a positive effect of arable land amount on cabbage aphid and spiders in July/August. The covariables regarding crop protection nets had species specific effects, thereby extending results of chapter 3 by the comparison of finer mesh sizes and net removal.

4.1. Landscape effects

4.1.1. Cabbage whitefly (*Aleyrodes proletella*)

The abundances of all developmental stages of the cabbage whitefly in Brussels sprout fields increased with increasing oilseed rape area. This is in accordance with our first hypothesis and with findings in chapters 1, 2 and 3 (chapters 1 and 2 focussed on colonisation, chapter 3 on plants in Brussels sprout fields). Oilseed rape fields can support whitefly populations as habitats for overwintering and reproduction of the first generation before vegetable cabbages are planted (Belder *et al.*, 2008; Richter & Hirthe, 2014b). Colonisation of vegetable *Brassicas* takes place mainly in July when oilseed rape plants mature and dry (chapter 1). Results of the present chapter showed that oilseed rape area determined whitefly densities in Brussels sprout fields throughout the year including October, the month with highest whitefly densities. As oilseed rape fields are harvested in August, direct effects of oilseed rape in October are extremely unlikely. Thus, high oilseed rape area in the surroundings of Brussels sprout fields led to high colonisation rates by whiteflies in early summer and consequently to high whitefly densities during the course of the year.

No evidence for higher importance of upwind oilseed rape area could be detected contrasting with our second hypothesis and findings from chapters 1 and 2. In general, whitefly dispersal is supposed to be characterised by passive wind transport (Byrne *et al.*, 1996), while upwind flights are possible in slow wind speeds only (Byrne, 1999). Accordingly, we detected an increased importance of upwind area in chapters 1 and 2 when investigating colonisation of standardised monitoring plants. In this chapter, we analysed arthropod abundances in Brussels sprout fields, reflecting not only colonisation but also reproduction, mortality and emigration. Thereby wind effects on colonisation might have disappeared in time in Brussels sprout fields. Furthermore, lower standardisation of plants in the fields adds additional variation that may have disguised a high importance of upwind source habitats. Additionally, the landscape in distances larger than 1 km was shown to be of higher importance for colonisation of Brussels sprout fields than the landscape up to 1 km distance (chapter 2). Consequently, a weighting by prevailing wind directions is expected to increase the effect of oilseed rape area most effectively on radii larger than 1 km (unfortunately, data on landscape composition in landscapes larger than 1 km were available for 2012 only, see chapter 2).

4.1.2. Cabbage aphid (*Brevicoryne brassicae*)

The abundance of cabbage aphids showed a weak positive relation to arable land and no relation to the area of oilseed rape fields contrasting with our first hypothesis. A positive relation between oilseed rape area and cabbage aphid colonisation was found on standardised monitoring plants in 2012 (chapter 1), the year with the by far highest density of cabbage aphids (Fig. 4.1e). High cabbage aphid densities in 2012 and standardised conditions possibly made the effect of oilseed rape area significant (chapter 1), while lower cabbage aphid abundance in 2013 and 2014 and less standardised conditions in the Brussels sprout fields may have concealed this effect of oilseed rape in chapter 3 and the current chapter. Additionally, the importance of different source habitats for aphids can vary between years

(Vialatte *et al.*, 2007). The positive effect of area of arable land on cabbage aphid abundance may be explained by higher natural pest control in complex landscapes. Different natural enemies of aphids are shown to positively respond to landscape complexity and the presence of semi-natural habitats, which is often negatively related to and measured by the amount of arable land (Roschewitz *et al.*, 2005; Thies & Tscharntke, 2010; Chaplin-Kramer & Kremen, 2012). High abundance of natural enemies may restrict cabbage aphid populations in landscapes with low proportion of arable land, even if we could not detect any effect of the area of arable land on natural enemies in Brussels sprout fields.

Table 4.2 Summary of the results reported in Table 4.1 for cabbage whiteflies (CW), cabbage aphids (CA), peach-potato aphids (PPA), diamondback moths (DMB), syrphids, spiders and aphid parasitism rates (Para. rate). Landscape variables of importance were: area of oilseed rape [%] (OSR), arable land [%] (AL) and area of waysides [%] (WS). Significant landscape variables within the best models were tested with downwind weighting of habitats (down) and with upwind weighting of habitats (up) in addition to their unweighted version. Models included the following covariables: day of the sampling period (day), mesh size of nets (net_mw), presence/absence of nets (net_pa) and prey abundance (prey). The direction of the effects is indicated: either positive (pos.) or negative (neg.). In some sampling periods abundances were too low for the analysis (x).

Taxon	**Sampling period**		
	'June/July'	'July/Aug.'	'October'
CW clutches	OSR (pos.; wind: no, up, down) day (pos.)	OSR (pos.; wind: no, up) day (pos.)	x
CW larvae	x	OSR (pos.; wind: no, up) day (pos.)	OSR (pos.; wind: no, up)
CW adults	OSR (pos.; wind: no, up) day (pos.)	OSR (pos.; wind: no, up) day (pos.)	OSR (pos.; wind: no, up)
CW sum	OSR (pos.; wind: no, up, down) day (pos.)	OSR (pos.; wind: no, up) day (pos.)	OSR (pos.; wind: no, up)
CA	x	AL (pos.; wind: no) net_mw (pos.)	day (neg.)
PPA	x	x	x
DBM	x	day (neg.) net_mw (neg.)	x
syrphids	x	prey (pos.)	x
spiders	x	AL (pos.; wind: no, up, down) day (pos.)	day (neg.) net_pa (neg.)
Para. rate	x	-	-

4.1.3. Peach-potato aphid (*Myzus persicae*)

None of the landscape variables affected peach-potato aphid abundance. Peach-potato aphids have a very broad range of summer hosts including crops, ornamentals and wild plants from over 40 plant families (Capinera, 2001). Therefore, lots of different habitats such as crop fields (e.g. oilseed rape, beet and potato fields), home gardens and semi-natural habitats can affect peach-potato aphid populations simultaneously. Also overwintering of the peach-potato aphid may depend on different habitats in the study region. The main winter host of the peach-potato aphid (*Prunus persicae*) is rarely grown in the study region, but other less preferred *Prunus* species are available (Emden *et al.*, 1969). In addition, it can overwinter as adult on plants in heated human buildings (e.g. greenhouses) and outside in mild winter (Emden *et al.*, 1969). In summary, several divergent habitats affect peach-potato aphids in summer and winter, leading to no outstanding effect by the investigated landscape elements on this species.

4.1.4. Diamondback moth (*Plutella xylostella*)

In contrast to our hypothesis, expecting a negative effect of arable land, we did not detect any landscape effect on the diamondback moth. Although diamondback moth is one of the economically most important pests worldwide (Zalucki *et al.*, 2012), little is known about the effects of specific landscape elements on diamondback moths (Furlong *et al.*, 2013). A comparably low importance of the local landscape can be explained by the facts that (1) the species does not hibernate in the study region but immigrates from regions with milder winters each year (Furlong *et al.*, 2013) and (2) individuals show only low willingness to move once they are established in a crop (Mo *et al.*, 2003). However, positive effects of permanent habitats on colonisation by the diamondback moth could be shown in chapter 1 and were explained by a high food offer for adults in these habitats. Less standardisation of sampled plants in the Brussels sprout fields as well as different population development over time might have led to no significant landscape effects.

4.1.5. Syrphids

According to our second hypothesis and to results regarding colonisation of monitoring plants in chapter 1, the abundance of immature syrphid stages in Brussels sprout fields was not related to landscape complexity or any other of the investigated landscape variables. Other studies suggest that the abundance of aphidophagous syrphids increases in landscapes with high proportions of arable land supporting their offspring with food (Haenke *et al.*, 2009; Meyer *et al.*, 2009). In contrast, Chaplin-Kramer & Kremen (2012) found high syrphid densities in complex landscapes with low proportion of arable land. As syrphids are highly mobile, potential relations to landscape elements may be temporarily restricted. This was already shown for effects of oilseed rape fields on syrphids, being limited to their flowering time in April/May (Riedinger *et al.*, 2014).

4.1.6. Spiders

Spider abundance increased significantly with the percentage area of arable land in July/August. This is surprising, as often less managed habitats such as field margins or grasslands are seen as important source habitats of spiders (Schmidt & Tscharntke, 2005; Geiger *et al.*, 2009). Annual spider dispersal by ballooning shows two peaks: the first between June and July and the second between September and October (Blandenier & Fürst, 1998; Blandenier, 2009). The first peak may be raised by high emigration from crop fields that are harvested in July (Blandenier & Fürst, 1998) and explains the positive effect of percentage area of arable land on spider abundances in Brussels sprout fields in July/August. As models including arable land with and without weighting by wind were of similar quality, also wind independent dispersal by crawling spiders may have contributed to spider abundances in

Brussels sprout fields in July/August. The second peak in spider dispersal is supposed to be caused by physiological and meteorological reasons (Blandenier, 2009) and explains why the effect of arable land on spider abundance in Brussels sprout fields disappeared in October.

4.1.7. Aphid parasitism

Aphid parasitism was related to none of the investigated variables. In contrast, parasitism rates of aphids in cereals and of pollen beetles in oilseed rape fields are shown to increase with increasing landscape complexity in landscapes of 1 – 2 km radius (Roschewitz *et al.*, 2005; Thies & Tscharntke, 2010). Flower rich habitats may support most parasitoids in providing nectar, which in addition to honeydew from phloem sucking insects increases longevity and fecundity of parasitoid adults (Singh *et al.*, 2000; Tylianakis *et al.*, 2004). The parasitic wasp *Diaeretialla rapae* is the only parasitoid of the cabbage aphid and an important parasitoid of the peach-potato aphid (Hafez, 1961; Pike *et al.*, 1999; Desneux *et al.*, 2005; Neuville *et al.*, 2016). *D. rapae* is known for a low tenacity for sustained flight (Sheehan & Shelton, 1989; Vaughn *et al.*, 1996; Vaughn & Antolin, 1998), but even testing for landscape effects in a 500 m radius around the study fields remained without significant effects (unpublished data). The surrounding landscape might be of low importance for *D. rapae* populations as the investigated organic horticultural farms providing nectar from weeeds and honeydew from phloem sucking insects at any time of the growing season.

4.2. Covariables

The following covariables were included: (1) the day of the sampling period to account for short term temporal changes in arthropod abundances during the 24 to 37 days lasting sampling periods, (2) mesh size or presence of crop protection nets and (3) prey / host availability for natural enemies. The consideration of day of the sampling period to account for short term temporal changes was useful, as it had significant effects on the abundance of some of the investigated taxa. Also covariables regarding crop protection nets and prey / host availability for natural enemies showed significant effects and will be discussed in more detail, as they are substantively meaningful for sustainable crop protection concepts.

Nets included in this study had a relatively fine mesh size from 0.8 mm to 1.35 mm (eight farms each) to the widest mesh size of 1.75 mm (one farm). In contrast to chapter three, comparing the effects of fine and wide meshed nets in 2014 (0.8 mm vs. 7 mm mesh size), cabbage whitefly and spider abundances were not affected by net mesh size, probably due to the smaller difference in net mesh size in this chapter. On the contrary, cabbage aphid abundance increased with net mesh size in July/August in this chapter, while no significant effects were shown by comparing fine with wide meshed nets in 2014. However, a trend towards higher cabbage aphid densities under 7 mm compared to 0.8 mm nets in August 2014 was visible (Fig. 3.1 in chapter 3), even though aphid numbers were generally low in 2014. Other studies recommend net mesh sizes from 0.5 mm (Hommes, 1993) to 0.6 mm (Dixon, 2007) and 1.35 mm (Ester *et al.*, 1994) against aphids in vegetable *Brassicas*. Our findings suggest that in particular nets with a mesh size ≥ 1.35 mm are permeable to aphids in vegetable *Brassicas*. Diamondback moth abundance showed a weak negative effect by net mesh size. Although chapter 3 showed no significant effect, a similar trend of higher diamondback moth abundance under fine meshed nets was visible (Fig. 3.1b in chapter 3). In general, nets are shown to effectively reduce diamondback moth in vegetable *Brassicas* (Martin *et al.*, 2006). However, it may be possible that diamondback moths which once reached Brussels sprout plants under the net (e.g. during weeding in the early morning) find in particular under fine meshed nets suitable conditions for population growth such as protection from natural enemies. This is supported by findings from chapter 3 with lower densities of spiders (a highly abundant group of natural enemies in our studies) under 0.8 mm than under 7 mm nets in August. However, in the present chapter were found higher densities of spiders in Brussels sprout fields still covered by nets than under uncovered fields in October. But here as well might be a potential reason the (intraguild) predation e.g. by birds, which are effectively deterred by nets independently from their mesh size (Mooney *et al.*, 2010).

The abundance of immature syrphid stages was related to prey availability according to findings in chapters 1 and 3. *Episyrphus balteatus*, the most abundant syrphid in Brussels sprout fields of the study area (Hafez, 1961; Laurenz & Meyhöfer, 2015b), is known to be attracted by high aphid densities (Budenberg & Powell, 1992; Verheggen *et al.*, 2008). In our studies, prey abundance was clearly dominated by cabbage whiteflies (96 % whiteflies and 4 % aphids), suggesting that syrphids are not only attracted by high aphid (Budenberg & Powell, 1992; Verheggen *et al.*, 2008) but also by high cabbage whitefly densities. This was affirmed by additional analyses replacing prey availability (aphids and whiteflies; p = 0.017, AICc = 74.8) by only whitefly or aphid prey, showing that whitefly prey explained syrphid abundance similarly well (p = 0.017, AICc = 74.1) but much better than aphid prey (p = 0.212, AICc = 79.0). Interestingly, in contrast to findings from chapter 3, spiders were not related to prey densities – or, more precisely, this effect indeed was significant in July/August when separately tested (p-value = 0.016, estimate ± SE = 0.218 ± 0.082), but the model quality clearly remained behind the stated models without this variable (ΔAICc = 2.87). This positive effect of prey availability might have been displaced by the positive effect of arable land area in July/August.

4.3. Conclusion

This chapter deals with the relation between different landscape elements and the occurrence of pests and natural enemies under production situation in Brussels sprout fields. Colonisation of Brussels sprout plants by inter alia cabbage whitefly increased with oilseed rape area, offering host plants to all investigated pest species (chapters 1 and 2). The positive effect of oilseed rape area on this most abundant pest in our studies persisted under crop production situation in Brussels sprout fields regarding all different developmental stages throughout the cropping season. This showed that landscape effects on colonisation in early summer can determine pest densities even shortly before harvest. The damage caused by whiteflies is directly related to their abundance (Richter & Hirthe, 2013). Therefore, the need for crop protection and the cost effectiveness can be directly linked to the area of oilseed rape in the surrounding landscape for the production of *Brassica* vegetables which are sensitive to damage by the cabbage whitefly. Chapters 1 and 2 showed a higher importance of upwind oilseed rape area for colonisation by cabbage whiteflies, indicating wind dispersal by whiteflies for radii ≥ 1 km, as well as effects of divergent landscape elements on cabbage aphids and diamondback moths. These relations were no longer present in this chapter, probably due to less standardised and population growth affected crop production situation in Brussels sprout fields. Furthermore, cabbage aphid abundance responded positively to the amount of arable land implying an underlying negative effect of landscape complexity. Generally, complex landscapes are shown to boost natural enemy abundance, even if no effects of landscape elements on syrphids and aphid parasitoids (parasitism rate) were found in this chapter. In contrast, positive effects by the area of arable land on spider abundance in July/August were shown, most probably related to spiders that emigrated from harvested crop fields. Even though spiders always were an abundant group of natural enemies, the similar abundant syrphid larvae showed most potential for control of whiteflies, as their abundance responded positively to availability of this by far most abundant pest species on all farms during three years.

Synthesis

The **overarching objective** of the joint project 'reliability through sustainable crop protection' within the 'competence network: value chain horticulture' (Kompetenznetz: Wertschöpfungskette Gartenbau [WeGa]) was to develop environment friendly, holistic crop protection strategies. This thesis contributes to this aim by gathering knowledge on potential source habitats for pests of vegetable *Brassicas* and their natural enemies in the landscape surrounding Brussels sprout fields. It further shows how wind, temperature and crop cover nets influence effects of source habitats. This synthesis highlights the main results of the thesis, relates them to associated bachelor and master theses, argues how results of different chapters add up to a coherent picture and discusses how these findings can contribute to environment friendly holistic crop protection strategies.

The **first chapter** deals with effects of different potential source habitats on colonisation of young Brussels sprout plants by different pests and their natural enemies. Colonisation by the cabbage whitefly (*Aleyrodes proletella*) increased with increasing upwind oilseed rape area. The importance of oilseed rape for the cabbage whitefly was already suggested (Belder *et al.*, 2008; Richter & Hirthe, 2014a). Accordingly, a master thesis linked to our study shows that cabbage whitefly populations in oilseed rape and Brussels sprout fields are genetically similar (Hüweler, 2015). Several studies revealed the importance of wind in dispersal of different whitefly species (Byrne & Bellows, 1991; Byrne *et al.*, 1996). We merged these findings and showed that 66 % of the variation in colonisation of young Brussels sprout plants by the cabbage whitefly was explained by upwind oilseed rape area in a 1 km radius around the study site and by temperature.

Colonisation by cabbage aphids (*Brevicoryne brassicae*) was found to increase with increasing oilseed rape area downwind from the study sites (chapter 1). This is surprising as, similar to whiteflies, aphids are known to use downwind drift in their dispersal and to have limited abilities to fly upwind (Loxdale *et al.*, 1993; Compton, 2002). However, also upwind flights towards olfactory stimuli are reported for aphids, but there is no knowledge about how far aphids follow olfactory host cues (Döring, 2014). Results of chapter 1 are a first hint on upwind flights by aphids for a surprisingly large distance of 1 km. Another master thesis associated with our study aimed to assess the genetic exchange, i.e. similarity, of populations in Brussels sprout and oilseed rape fields (Yakti, 2013). Sadly, a reliable genetic comparison of cabbage aphid populations failed due to technical difficulties with the use of microsatellite markers. However, the extensive optimisation of the procedure now allows for genetic comparisons of cabbage aphid populations by microsatellites.

Another project associated master thesis showed, based on kohlrabi, that colonisation by cabbage root fly (*Delia radicum*) correlates with oilseed rape area in 500 m and 1,000 m radii around kohlrabi fields too (Lessing, 2016). Contrastingly, no effect of oilseed rape area in 50 – 500 m distance on colonisation of broccoli fields by cabbage root flies in northern Brittany, France, was found (Josso *et al.*, 2013). Likewise, no significant effects by oilseed rape area, but marginal positive effects by downwind permanent habitats offering high amount of nectar resources even beyond flowering period of oilseed rape, were shown in chapter 1 for colonisation of Brussels sprouts by diamondback moths (*Plutella xylostella*).

The colonisation of Brussels sprouts by syrphid eggs and larvae did not respond to any of the tested potential source habitats. Instead, syrphids significantly increased with increasing number of prey insects, which were dominated by the cabbage whitefly (88 %). Syrphids are known to be important natural enemies of aphids (Tenhumberg & Poehling, 1995). The most abundant syrphid species in agricultural landscapes in Germany, including Brussels sprout fields, is the marmalade hoverfly (*Episyrphus balteatus*) (Hafez, 1961; Freier *et al.*, 2007; Haenke *et al.*, 2009). While this species is known to be attracted by honey dew from aphids and by high aphid densities (Budenberg & Powell, 1992; Freier *et al.*, 2007), chapter 1 shows that also cabbage whitefly densities positively affect syrphid abundance.

The **second chapter** focuses on cabbage whitefly as the most numerous pest species in Brussels sprout fields of our study. Effects of oilseed rape were intensively investigated on different spatial scales up to a distance of 8 km. Thereby special attention was payed to effects of upwind flights towards olfactory stimuli and passive wind dispersal, possibly acting in opposite directions. The results showed that upwind oilseed rape area in a radius of 5 km explained colonisation best. The finding that cabbage whiteflies disperse over relatively large distances is supported by the genetic similarity of geographically separated whitefly populations (Hüweler, 2015). The oilseed rape area in the closer vicinity of 200 m to 1,000 m around the study sites was not correlated to colonisation by cabbage whitefly, showing that the local landscape is of minor importance for its colonisation of vegetable *Brassicas*.

The **third chapter** evaluates the effect of crop cover nets, a common preventive crop protection measure, on different pests and their natural enemies in Brussels sprout fields. Commonly used 0.8 mm nets, compared to wide meshed 7 mm nets, reduced colonisation by cabbage whitefly and spiders early in the year. This effect of nets decreased during the growing season. Additionally and in accordance to chapters 1 and 2, we could detect a positive effect of oilseed rape area on cabbage whitefly presence, which was most pronounced late in the year.

The **fourth chapter** investigates to what extend results on the factors that drive colonisation of highly standardised monitoring plants in early summer (chapters 1 and 2) can be transferred into crop production situation in Brussels sprout fields. A high generality of results was ensured by including data from three years, while four pest species and three groups of natural enemies were considered as well as an extended set of landscape variables compared to previous chapters. The positive effect of oilseed rape area on the most abundant pest in our studies, cabbage whitefly, persisted under crop production situation in Brussels sprout fields throughout the cropping season. This showed that landscape effects on colonisation in early summer can determine pest densities even shortly before harvest. Thus, the need for crop protection and the cost effectiveness can be directly related to the area of oilseed rape in the surrounding landscape for the production of *Brassica* vegetables which are sensitive to damage by the cabbage whitefly. Effects of prevailing wind directions as well as of divergent landscape elements on colonisation by different pests shown in chapters 1 and 2 were no longer present, probably due to less standardised and population growth affected crop production situation in Brussels sprout fields. Also in this chapter, abundance of syrphid larvae responded positively to whitefly prey availability.

Results of the different chapters are widely consistent and build a largely **coherent picture** particularly for the cabbage whitefly, being the most abundant pest throughout the cropping season in all years and consequently involved in all four chapters of the thesis. Colonisation of Brussels sprouts by this species was positively affected by the amount of oilseed rape in the surrounding landscape, while the wider landscape was of higher importance compared to radii ≤ 1 km (chapters 1 and 2). Consideration of prevailing wind directions pointed towards passive wind dispersal for distances of about 5 km (chapter 2). The positive effect of oilseed rape area on colonisation of Brussels sprouts by cabbage whiteflies (chapters 1 and 2) also persisted under less standardised crop production situation in Brussels sprout fields throughout the cropping season (chapters 3 and 4). Thus, as crop damage by cabbage whitefly is known to be closely linked to its abundance (Richter & Hirthe, 2013), the need for crop protection can be directly related to the area of oilseed rape in the surrounding landscape.

Comparing the importance of different radii in different chapters (comparison of single radii ≤ 1 km in chapter 1, 2 and 4; comparison of combinations of radii ≤ 8 km in chapter 2), we found a remarkable part of cabbage whitefly abundance explained by oilseed rape area in 1 km radius in chapter 1 (as well as in chapters 3 and 4). This finding seems to contrast with the findings from chapter 2, showing that the explained variability is only high for oilseed rape in radii > 1 km. This contrast bears from the special situation around one study site, which was included in analyses of chapter 2, but not in chapters 1, 3 and 4. While the oilseed rape area in 1 km radius approximately reflected the oilseed rape area of the wider radii for all other study sites, the landscape around this particular study site abruptly changed from high amount of oilseed rape in < 1 km to low amount of oilseed rape in > 1 km distance from the study site. Thus, oilseed rape amount in 1 km radius around study sites was a good predictor for cabbage whitefly colonisation as long as it approximately reflected the wider landscape. This shows that cabbage whiteflies colonise Brussels sprout fields mainly for distances > 1 km as shown in chapter 2 and supported by the results of Hüweler (2015) (see above). Furthermore, results of chapters 1, 3 and 4 do not lose in validity due to the exclusion of the only study site of which the local landscape not even roughly reflected the composition of the wider landscape.

Recommendations for the development of crop protection strategies

Oilseed rape fields in distances > 1 km affected colonisation of Brussels sprouts by cabbage whiteflies strongest, while oilseed rape area in the closer surroundings was shown to be of lower importance. Thus, there is no need for farmers of vegetable *Brassicas* to avoid oilseed rape fields in the local surroundings, i.e. in up to 1 km distance (possible exception might be oilseed rape fields directly bordering vegetable *Brassicas*, pers. observation). If much oilseed rape is grown in the wider landscape *Brassica* vegetables should be expected to be colonised by pests in high numbers, particularly by cabbage whiteflies. Farmers who still decide to grow *Brassica* varieties sensitive to cabbage whitefly (such as Brussels sprout, kale or savoy cabbage) have to accept a higher need for crop protection measures such as promotion of natural enemies or use of crop cover nets.

Several *Brassica* pests can be effectively reduced by crop cover nets (Hommes, 1993; Ester *et al.*, 1994). Nets with a mesh size of 0.8 mm compared to 7 mm mesh width effectively reduced colonisation by cabbage whitefly early in the season, while no effects were detected in October (chapter 3). Unfortunately, the use of close meshed (0.8 mm) compared to wide meshed crop cover nets (7 mm) also reduced the presence of natural enemies such as spiders and, as a trend, also aphid parasitism (chapter 3). However, these protective effects by nets disappeared more and more in the later season. Due to potential effects of crop cover nets on pest and natural enemy abundance, we included only Brussels sprout fields using the more common close meshed nets (0.8 mm vs. 1.35 mm) in analyses of chapter 4 and additionally used mesh width as a covariable. Results suggest lower cabbage aphid abundance and higher diamondback moth abundance under 0.8 mm nets compared to 1.35 mm nets in mid cropping season as well as less spiders on Brussels sprout plants if nets were removed in October. However, the differences in close meshed crop cover nets used as covariables in chapter 4 should not be overestimated as the range in mesh width was small and design less balanced compared to chapter 3, of which mesh width was a focal issue. In conclusion, closed meshed nets seem to hinder colonisation by some species and to favour infestation of plants by other species probably due to lowered pressure by natural enemies. However, almost all effects of nets disappeared in the later season (chapters 3 and 4). One important reason may be that farms need to remove nets frequently for weed management, allowing pests and natural enemies to enter or escape from plants.

Different strategies may increase the efficacy of crop cover nets and overcome the shortcomings described above. First, potential reasons leading to decreased efficacy of nets during the season need to be identified and minimised; theese may be that: (i) 0.8 mm nets are not completely insurmountable to cabbage whiteflies as shown by an project associated bachelor thesis (Lessing, 2013), (ii) nets are installed belatedly that is not directly after planting, (iii) worn nets with holes are used, (iv) nets are not properly fixed to the ground and lifted by wind or growing plants, (v) temporary net removal for weeding takes place at inadequate times, while the optimal time for net removal is supposed to be cool and cloudy mornings when pests such as cabbage whitefly and cabbage root fly show low flight activity (Stein, 1958; Hawkes, 1972). All these potential reasons for decreased efficacy of crop cover nets were observed in the field and often result from compromises demanded by farming practice. However, if compromises should be accepted consciously and not unintentionally lead to inefficacy of nets, more knowledge on landscape- and pest-specific consequences of different mesh widths, times of net installing and removal, manner of temporal net removal for weeding and degree in accuracy is needed. Second, the disadvantage that crop cover nets can reduce natural enemy abundance could be compensated by releasing natural enemies under nets. However, this technic is only poorly approved up to now and needs further optimisation (Saucke *et al.*, 2011). Third, a useful strategy might be to use nets in the early season for reduction of initial colonisation by pests, while they are replaced by other crop protection measures such as the support of natural enemies during the later season. This strategy has the advantage to hinder colonisation by pests early in the year, when natural enemies are rare, and to allow natural enemies to attack pests later in the year when natural enemies are more abundant (Tenhumberg & Poehling, 1995). Furthermore, the early support of natural enemy populations e.g. by creation of flower strips close to the crop might effectively suppress pest populations as soon as nets are removed.

Flower strips are often recommended to support adult parasitoids and syrphids in offering nectar (Haenke *et al.*, 2009; Balmer *et al.*, 2013). Syrphids are effective natural enemies of aphids (Tenhumberg & Poehling, 1995), thereby showing a strong numerical response to aphid numbers (Freier *et al.*, 2007). Although it is shown that some syrphid species prey on whiteflies including *A. proletella* (Evans, 2007; Rijn *et al.*, 2008), little is known on their efficacy in pest control regarding whiteflies. In chapters 1, 3 and 4 was shown that abundance of syrphid larvae, the most abundant generalised predators besides spiders, was driven by the abundance of prey organisms, more precisely by the abundance of whiteflies (chapter 4). Thus, syrphids may have more potential to control cabbage whitefly populations than previously assumed.

The calcid wasp *Encarsia tricolor* is an effective parasitoid of the cabbage whitely, reaching parasitism rates of more than 90 % in extreme cases (Saucke *et al.*, 2011). A median cabbage whitely parasitism rate of 1.7 % (min. = 0 %, max. = 44 %) had been observed at our study sites in October (Ludwig *et al.*, 2014). *E. tricolor* does not benefit from oilseed rape fields contrary to their host *A. proletella*. This is because cabbage whiteflies occur in winter oilseed rape fields only as adults in autumn and winter (since winter oilseed rape is sown in autumn only, chapter 1 Table 1.1, Belder *et al.*, 2008) and *E. tricolor* hibernates as pupa inside the larvae skin of it hosts (Arzone, 1977). However, *E. tricolor* could overwinter on remnants of vegetable *Brassicas*, if remnants are not entirely ploughed under, as leaves of Brussels sprouts often contain a large number of parasitised whitefly larvae (pers. obs.). Therefore, remnants of vegetable *Brassicas* could be stored during winter and placed close to a Brussels sprout field in the following year, ensuring high parasitism rates. Thereby, colonisation of crops by pests overwintering on these leaves could be avoided by covering the exposed leaves with nets of mesh sizes just large enough for the small parasitoids to pass, but too small for Lepidoptera. Furthermore, leaves could be exposed in a certain distance to the field to ensure that un-winged fundatrices, hatched from overwintering cabbage aphid eggs, are not able to reach the crop. Another potential strategy to support overwintering of *E. tricolor* close to the crop is the offer of alternative indigenous winter hosts which hare harmless to the cultivated crop (Laurenz & Meyhöfer, 2015a), such as honeysuckle whitefly (*Aleyrodes lonicerae*) and ash whitefly (*Siphoninus phillyreae*) (Evans, 2007; Heraty *et al.*, 2007; Noyes, 2016). A disadvantage may be that they are minor pests of strawberries (*A. lonicerae*), apple and *Prunus* species (*S. phillyreae*).

Though cabbage whiteflies were the by far most abundant pest in our studies, aphid species such as cabbage aphid and peach-potato aphid (*Myzus persicae*) were observed frequently (e.g. chapter 4). A potential method of environment friendly crop protection may be crop cover nets (Hommes, 1993; Ester *et al.*, 1994). However, we found partly opposing effects of crop cover nets on aphids: while abundance of peach-potato aphids was higher under 0.8 mm compared to 7 mm nets, the cabbage aphid abundance showed no differences (chapter 3) but seemed to be less abundant under 0.8 mm compared to 1.35 mm nets (chapter 4). Furthermore, close meshed nets seem to prevent aphid parasitoids from pest control, even if the trend towards lower parasitism rates under close meshed nets was not significant (chapter 3). Consequently, there is need to improve the use of nets in farming practice and to develop further environment friendly crop protection strategies for *Brassica* crop production.

Although differing results on the reaction of *B. brassicae* to odours are shown (Nottingham *et al.*, 1991; Nottingham & Hardie, 1993), our results indicate that cabbage aphids are attracted by olfactory host cues (chapter 1). Consequently, olfactory orientation could be used to construct specific traps e.g. for monitoring or push and pull strategies (Döring, 2014). Aphids parasitoids, besides syrphid larvae, belong to the most effective natural enemies of aphids (Hafez, 1961; Desneux *et al.*, 2005). Parasitism rates can possibly be increased by release of parasitoids under crop protection nets or by support of their natural populations. Flower strips supply adult parasitoids with nectar, pollen and hosts for oviposition (Tylianakis *et al.*, 2004). However, it is uncertain if parasitoids leave flower strips in sufficient numbers to effectively control aphid populations in adjacent Brussels sprout fields. A project associated bachelor thesis compared aphid parasitism rates on standardised monitoring Brussels sprout plants within flower strips and adjacent Brussels sprout plots after releasing the parasitoid

Diaeretiella rapae (Brun, 2013). Interestingly, more aphids were parasitised on standardised monitoring plants in Brussels sprout plots than in flower strips, indicating a preference for hosts surrounded by an attractive 'scent cocktail' produced by aphids and plants in Brussels sprout plots (Reed *et al.*, 1995). Thus, flower strips can be an crop protection strategy in promoting parasitoids as well as syrphids (Tylianakis *et al.*, 2004; Haenke *et al.*, 2009), two important antagonists of major *Brassica* crop pests such as aphids and cabbage whiteflies.

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Appendix A

Appendix A.1: Location of study sites in 2012

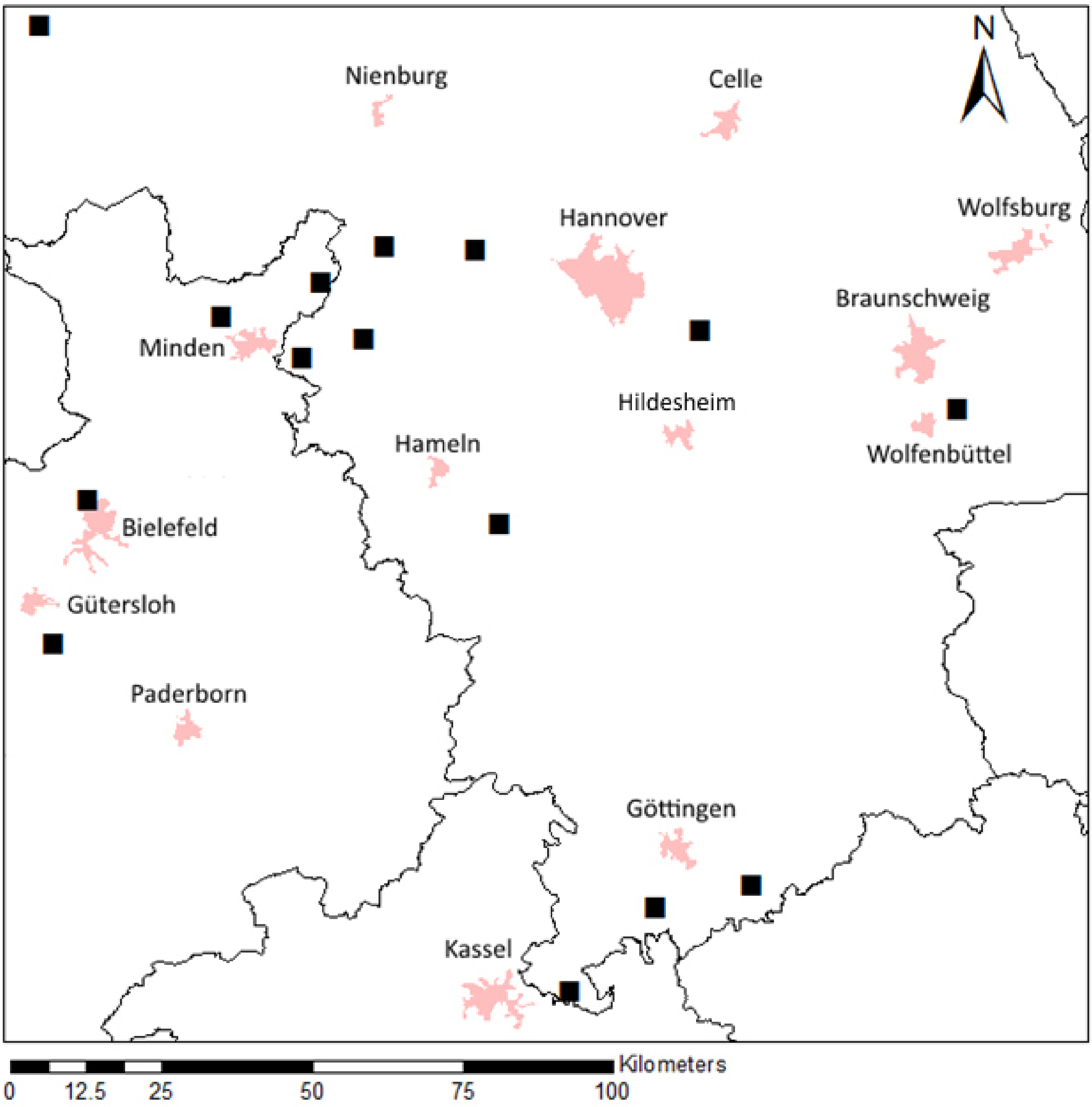

Fig. A.1 Location of study sites (filled squares) in southern Lower Saxony and northern North Rhine-Westphalia, Germany.

Appendix A.2: Study site exclusion

We excluded three study sites from the dataset. Two study sites on which weather recording failed were excluded to increase comparability between analyses with and without weather data. The third study site was an outlier in preliminary analyses of effects of oilseed rape area on colonisation of monitoring plants. Therefore we checked the landscape configuration surrounding this study site: While the 1 km radius was dominated by agricultural land use, the wider surroundings consisted on three sides of a wooded mountain-ridge and on the fourth side of a city. This special situation may have hindered colonisation of the monitoring plants (and other plants within the 1 km radius) by pests and natural enemies from agricultural landscape around the 1 km radius. In no other study site the landscape configuration changed that dramatically from inside to outside the 1 km radius. Additionally, data collection at this study site was influenced by extraordinary heavy rain showers in July that partly destroyed the monitoring plants. Consequently we excluded it from analyses.

Appendix A.3: Egg number per *Aleyrodes proletella* egg clutch

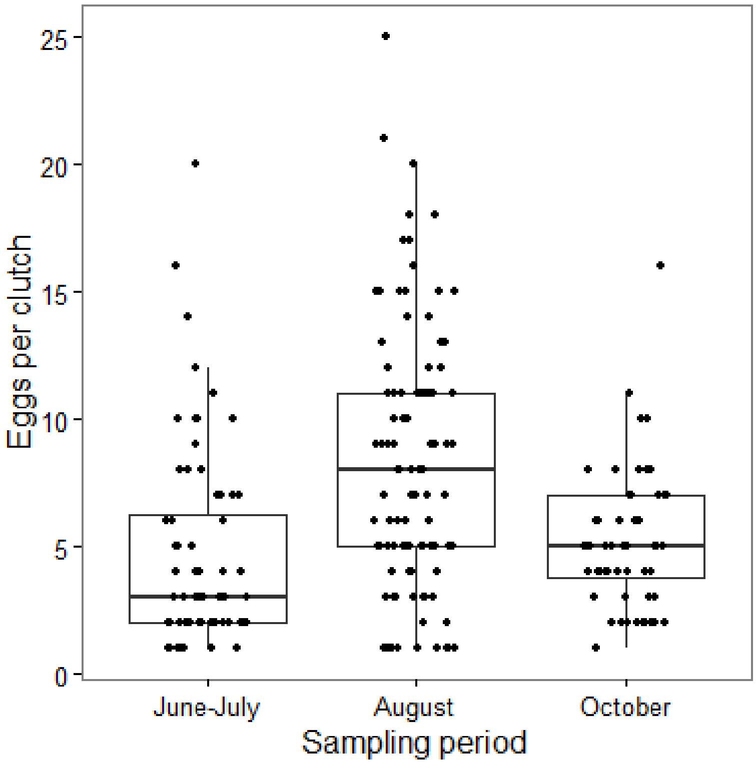

Fig. A.3 Boxplot-diagram showing egg numbers per *Aleyrodes proletella* egg clutch on Brussels sprout leaves at different times of the year 2013. Each dot represents one egg clutch. Dots are vertically jittered. Mean for June-July = 4.678, August = 8.273 and October = 5.232

Appendix A.4: Correlation between explanatory variables

Table A.4 Pearson's correlation between explanatory variables. T.day.10 and T.day.15 = degree days from 1 h after sunrise to 1 h before sunset with a threshold of 10 °C and 15 °C, respectively; T.night.7 = degree days from 1 h after sunset to 1 h before sunrise with a threshold of 7 °C. Coefficients of determination > 0.25 (|r| > 0.5, marked in bold) were used as threshold for collinearity (Dormann et al. 2013). Not displayed within the table is the coefficient of determination of > 0.01 for correlation between prey availability and T.day.15.

Landscape variable			Prey availability	T.day.10	T.day.15	T.night.7
Weighting by wind	Land use type	Radius (m)				
No weighting	oilseed rape	500	0.14	< 0.01	< 0.01	0.01
		750	0.22	0.02	< 0.01	0.02
		1000	**0.42**	0.04	0.03	0.06
	other annual crop fields	500	0.03	0.01	< 0.01	0.05
		750	0.10	0.01	< 0.01	0.07
		1000	0.10	0.02	< 0.01	0.06
	permanent habitat	500	0.13	< 0.01	< 0.01	0.03
		750	0.13	< 0.01	< 0.01	0.05
		1000	0.12	< 0.01	< 0.01	0.04
Upwind weighted habitats using wind by day	oilseed rape	500	0.13	0.01	< 0.01	
		750	0.19	0.06	0.02	
		1000	**0.43**	0.05	0.03	
	other annual crop fields	500	0.05	0.01	< 0.01	
		750	0.13	0.01	< 0.01	
		1000	0.13	0.03	0.01	
	permanent habitat	500	0.12	< 0.01	0.01	
		750	0.14	< 0.01	< 0.01	
		1000	0.13	0.01	< 0.01	

Table A.4 (continued):

Landscape variable			Prey availability	T.day.10	T.day.15	T.night.7
Weighting by wind	**Land use type**	**Radius (m)**				
Downwind weighted habitats using wind by day	oilseed rape	500	0.11	0.02	0.04	
		750	0.19	< 0.01	0.01	
		1000	**0.35**	0.01	0.01	
	other annual crop fields	500	0.02	0.02	< 0.01	
		750	0.08	0.02	< 0.01	
		1000	0.06	0.02	< 0.01	
	permanent habitat	500	0.10	< 0.01	< 0.01	
		750	0.10	0.01	< 0.01	
		1000	0.09	0.01	< 0.01	
Upwind weighted habitats using wind by night	oilseed rape	500				0.01
		750				0.01
		1000				0.10
	other annual crop fields	500				0.07
		750				0.07
		1000				0.07
	permanent habitat	500				0.03
		750				0.05
		1000				0.04
Downwind weighted habitats using wind by night	oilseed rape	500				< 0.01
		750				< 0.01
		1000				0.01
	other annual crop fields	500				0.08
		750				0.12
		1000				0.13
	permanent habitat	500				0.09
		750				0.15
		1000				0.13

Reference

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. (2013), Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36: 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Appendix B

Appendix B.1: Classification of the remote sensing data

Table B.1.1 Overview of the crop type classes and the number of objects used for training and validation.

Crop type class	Total	Training	Validation
Flower strip	13	9	4
Vegetable	65	44	21
Cereal	226	151	75
Potato	23	16	7
Cabbage	15	10	5
Maize	128	86	42
Oilseed rape	95	64	31
Beet	44	30	14
Other vegetation	14	9	5
Grassland	292	195	97

Table B.1.2 Overview of the calculated vegetation indices. The bands of the ETM+ were named according to the part of the spectra they represent (e.g.: BLUE = 0.45 µm - 0.52 µm; GREEN = 0.53 µm - 0.61 µm; RED = 0.63 - 0.69 µm; NIR (near-infrared) = 0.78 µm - 0.90 µm; L = 0.5). SAVI = 'Soil-adjusted Vegetation Index'; NDVI = 'Normalised Differenced Vegetation Index'; SR = 'Simple Ratio'.

Index	Equation	Reference
SAVI	$(L+1) * \frac{(NIR - RED)}{(NIR + RED + L)}$	Huete 1988
NDVI	$\frac{(NIR - RED\ )}{(NIR + RED\ )}$	Rouse et al. 1974
SR	$\frac{NIR}{RED}$	None

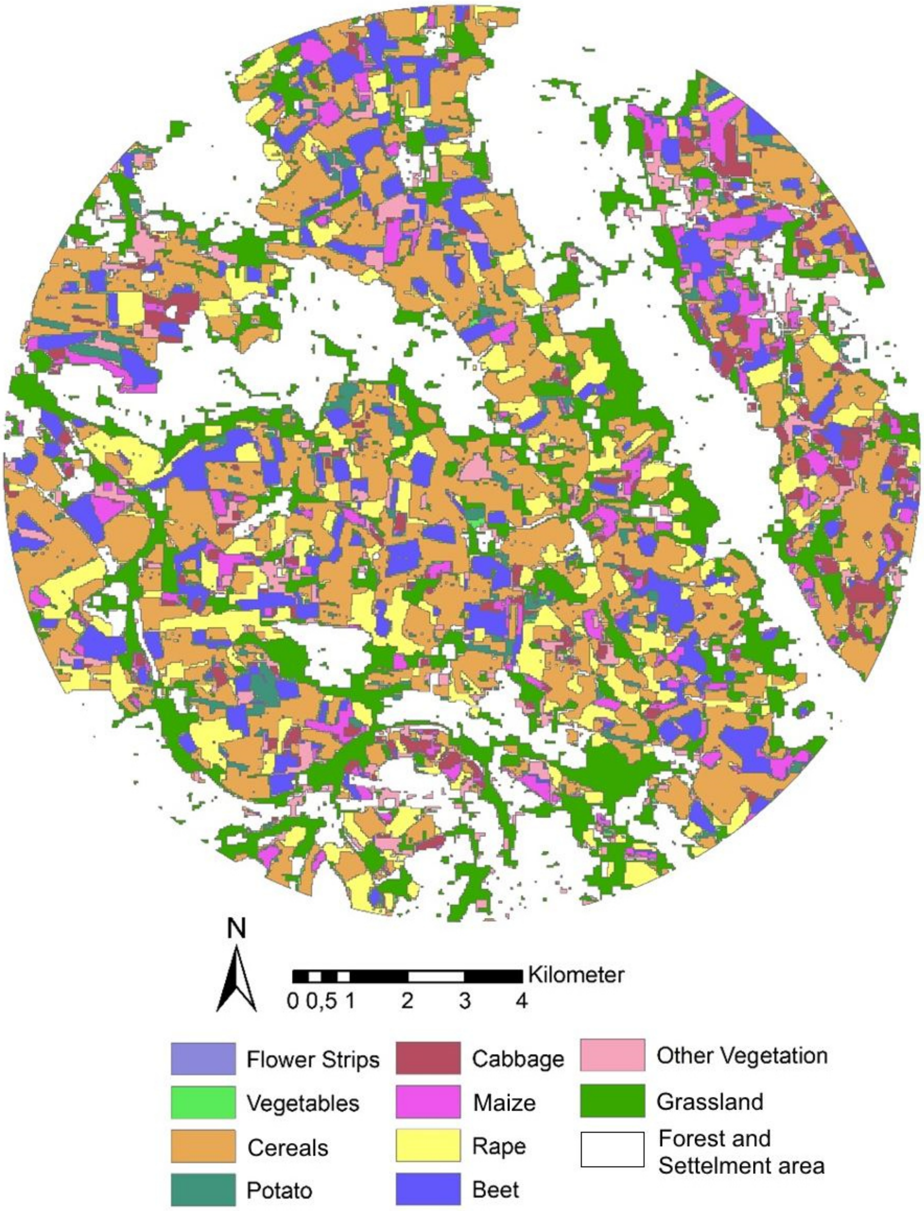

Figure B.1 Example of the classification result from an 8 km radius landscape around one of the study sites.

Table B.1.3 Accuracy table showing the producer's accuracy (percentage of the elements of a class that are correctly dedicated to that class), the user's accuracy (percentage of the elements dedicated to a class that really belong to that class), the overall accuracy and the Kappa coefficient (Congalton 1991).

Crop type classes	**Producer's accuracy [%]**	**User's accuracy [%]**
Flower strip	62.22	100.00
Vegetable	50.00	62.14
Cereal	86.34	79.96
Potato	78.92	96.68
Cabbage	94.92	73.68
Maize	71.56	79.31
Oilseed rape	89.51	88.96
Beet	85.44	92.05
Other vegetation	65.87	75.34
Grassland	83.77	61.47
Overall accuracy [%]	**79.89**	
Kappa coefficient	**0.76**	

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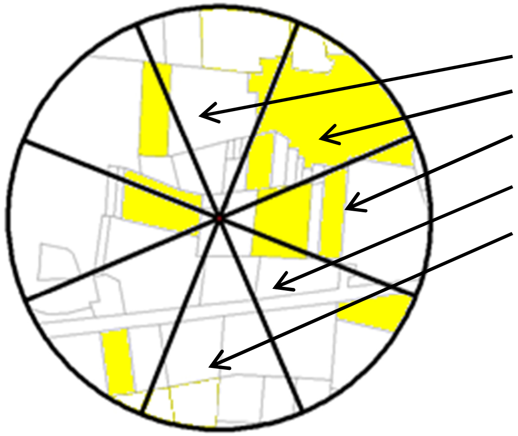
Appendix B.2: Example for the weighting by wind direction

Table B.2: Example for weighting by wind direction – downwind weighting of oilseed rape area in landscapes of 1 km radius around study sites.



Sector Direction	No. wind events towards the study site	Total wind events	Proportion of wind events	Oilseed rape area per sector [%]	Index of downwind weighted oilseed rape area per sector
	D	T	D/T	A	A*(D/T)
N	0	800	0.0000	0.153	0.00
NE	50	800	0.0625	66.208	4.14
E	100	800	0.1250	6.112	0.76
SE	120	800	0.1500	0.509	0.08
S	150	800	0.1875	0.509	0.10
SW	200	800	0.2500	0.000	0.00
W	100	800	0.1250	0.509	0.06
NW	80	800	0.1000	0.509	0.05
Percentage oilseed rape area of the 1 km radius landscape					9.314
Downwind weighted oilseed rape area of the 1 km radius landscape $\sum(A_i*(D_i/T))$				5.188	

Appendix B.3: Correlation between explanatory variables

Table B.3: Coefficients of determination (R^2) for the correlation between explanatory variables. We used $R^2 > 0.36$ ($|r| > 0.6$, marked in bold) as threshold for collinearity (Dormann et al. 2013).

			Amount of oilseed rape in local scale landscapes																	
			Without weighting by wind									**With downwind weighting of oilseed rape area**								
		Radius [m]	**1000**	**900**	**800**	**700**	**600**	**500**	**400**	**300**	**200**	**1000**	**900**	**800**	**700**	**600**	**500**	**400**	**300**	**200**
Amount of oilseed rape in wide scale landscapes	**Without weighting**	8000	0.05	0.01	0.00	0.01	0.03	0.03	0.06	0.09	0.12	0.01	0.00	0.01	0.03	0.05	0.07	0.08	0.09	0.11
		7000	0.03	0.00	0.01	0.02	0.04	0.05	0.06	0.09	0.12	0.00	0.00	0.02	0.04	0.06	0.07	0.08	0.09	0.13
		6000	0.02	0.00	0.02	0.03	0.05	0.05	0.06	0.07	0.12	0.00	0.01	0.03	0.04	0.06	0.07	0.07	0.09	0.13
		5000	0.01	0.00	0.02	0.04	0.06	0.06	0.06	0.08	0.13	0.00	0.02	0.04	0.06	0.07	0.08	0.08	0.09	0.16
		4000	0.03	0.00	0.01	0.02	0.03	0.03	0.03	0.04	0.09	0.00	0.00	0.02	0.03	0.04	0.04	0.04	0.05	0.11
		3000	0.08	0.02	0.00	0.00	0.01	0.00	0.01	0.01	0.06	0.03	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.06
		2000	0.24	0.16	0.11	0.06	0.05	0.04	0.02	0.00	0.03	0.10	0.05	0.04	0.02	0.01	0.00	0.00	0.00	0.03
		1000	**0.84**	**0.78**	**0.65**	**0.52**	**0.50**	**0.47**	**0.40**	0.32	0.12	**0.80**	**0.75**	**0.66**	**0.49**	**0.43**	**0.41**	**0.41**	**0.38**	0.28
	With upwind weighting of oilseed rape area	8000	0.02	0.00	0.00	0.02	0.03	0.03	0.04	0.04	0.03	0.00	0.00	0.01	0.03	0.04	0.05	0.05	0.06	0.00
		7000	0.00	0.00	0.02	0.03	0.05	0.04	0.04	0.04	0.02	0.00	0.02	0.03	0.04	0.05	0.06	0.06	0.06	0.00
		6000	0.00	0.01	0.03	0.05	0.06	0.05	0.04	0.03	0.04	0.01	0.03	0.04	0.04	0.05	0.06	0.06	0.06	0.01
		5000	0.00	0.01	0.03	0.05	0.07	0.06	0.04	0.04	0.06	0.01	0.04	0.05	0.06	0.06	0.07	0.07	0.08	0.01
		4000	0.02	0.00	0.01	0.03	0.04	0.03	0.02	0.02	0.05	0.00	0.01	0.02	0.03	0.04	0.04	0.04	0.05	0.00
		3000	0.07	0.02	0.00	0.01	0.01	0.00	0.00	0.01	0.03	0.02	0.00	0.00	0.01	0.01	0.02	0.02	0.02	0.02
		2000	0.19	0.15	0.10	0.05	0.04	0.04	0.02	0.00	0.01	0.07	0.04	0.03	0.01	0.00	0.00	0.00	0.00	0.07
		1000	**0.75**	**0.73**	**0.64**	**0.52**	**0.47**	**0.43**	**0.37**	0.32	0.14	**0.63**	**0.62**	**0.58**	**0.44**	**0.37**	0.34	0.33	0.31	0.63

Reference

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. (2013), Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36: 27–46. doi: 10.1111/j.1600-0587.2012.07348.x

Appendix C

Table C.1 Net mesh sizes used on different horticultural farms. Round brackets indicate that the net was removed by the farmer for the rest of the cropping period. Squared brackets indicate that parts of the nets were removed. - indicates that no data could be collected. Sampling events marked in bold were used for the statistical analysis.

Farm no.	June		August		October	
	Fine or intermediate mesh net [mm]	Wide mesh net [mm]	Fine or intermediate mesh net [mm]	Wide mesh net [mm]	Fine or intermediate mesh net [mm]	Wide mesh net [mm]
1	1.35	-	1.35	-	(1.35)	-
2	1.35	7	(1.35)	7	(1.35)	[7]
3	1.35	7	1.35	7	(1.35)	7
4	**0.8**	**7**	**0.8**	**7**	(0.8)	7
5	**0.8**	**7**	**0.8**	**7**	**0.8**	**7**
6	**0.8**	**7**	**0.8**	**7**	(0.8)	7
7	**0.8**	**7**	(0.8)	[7]	-	-
8	-	7	-	7	-	7
9	**0.8**	**7**	**0.8**	**7**	**0.8**	**7**
10	**0.8**	**7**	**0.8**	**7**	-	-
11	**0.8**	**7**	**0.8**	**7**	**0.8**	**7**

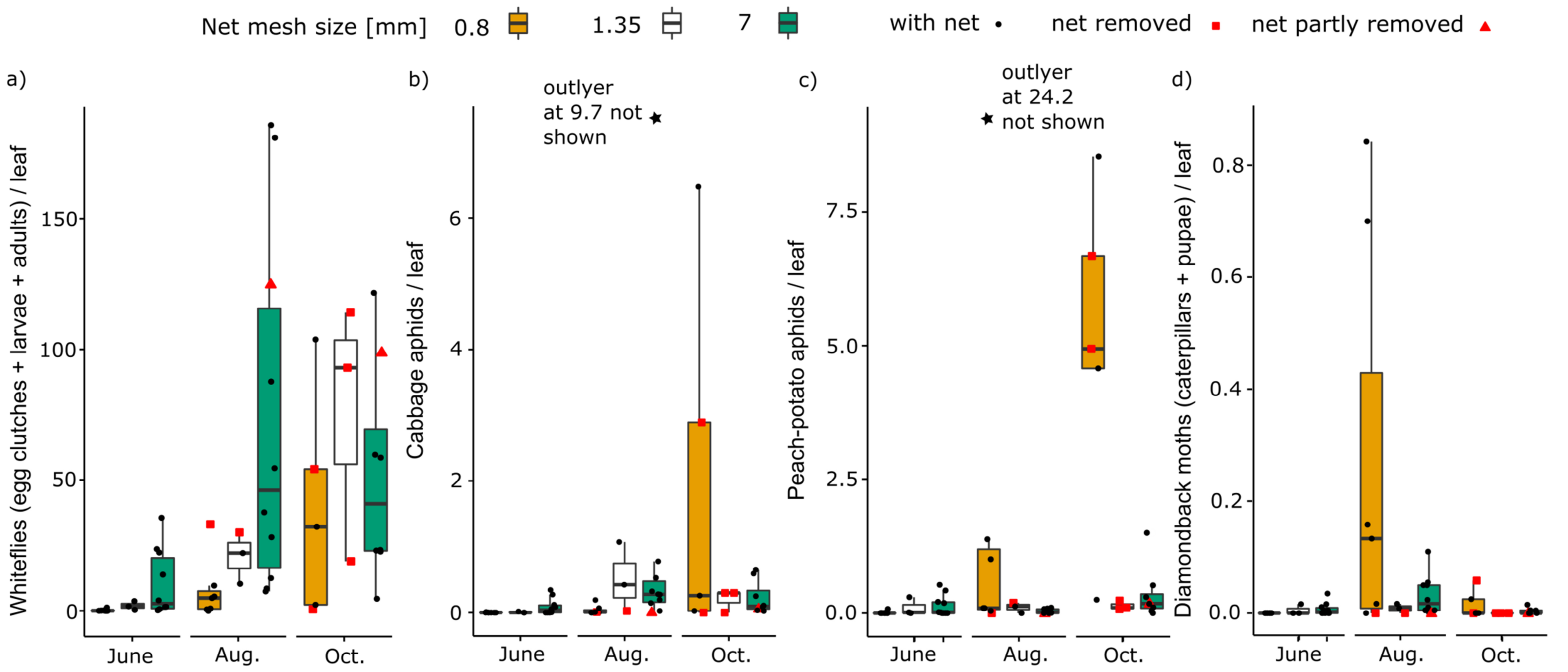


Fig. C.1 Population development of different pest insects on Brussels sprouts under nets of 0.8, 1.35 and 7 mm mesh size in June, August and October: a) cabbage whitefly, b) cabbage aphid, c) peach-potato aphid, d) diamondback moth. In addition to boxplot diagrams the underlying data points are shown with a horizontal jitter. Dots indicate study sites with nets on the crop, squares study sites with removed nets and triangles study sites with nets removed from 10 of 20 plants. In b) and c) one outlier each is not shown to give more space to the distribution of other points. All outliers were study sites with the nets on the crop.

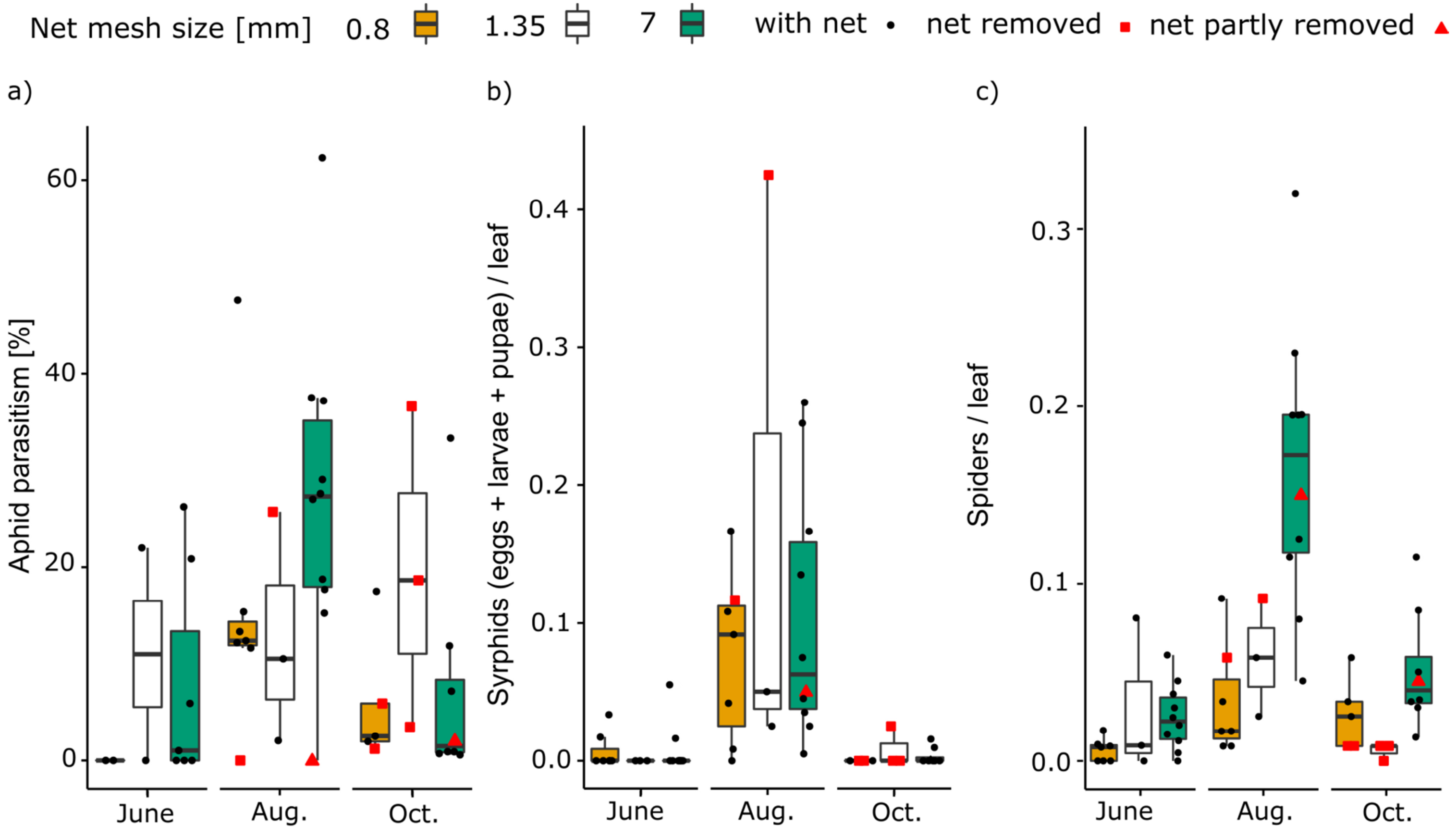


Fig. C.2 Population development of natural enemies on Brussels sprouts under nets of 0.8, 1.35 and 7 mm mesh size in June, August and October: a) aphid parasitism, b) syrphid eggs, larvae and pupae, c) spiders. In addition to boxplot diagrams the underlying data points are shown with a horizontal jitter. Dots indicate study sites with nets on the crop, squares study sites with removed nets and triangles study sites with nets removed from 10 of 20 plants.

Appendix D

Table D.1 Variation in sampling intensity among years and sampling periods. CW = cabbage whitefly, CA = cabbage aphid.

Year	Sampling period	No. of fields	Plants sampled per field	Leaves sampled per plant	Comment
2012	June/July	15	20	all	
2012	July/August	9 (all insects) +3 (CW +CA only)	20	10	10 plants / field if CW densities were high
2012	October	15	10	10	
2013	June/July	11	12	all	
2013	July/August	7	12	10	6 plants / field if CW densities were high
2013	October	10	12	10	6 plants / field if CW densities were high
2014	June/July	10	12	all	
2014	July/August	7	12	10	
2014	October	8	12	10	CW on only 6 plants / field if CW densities were high

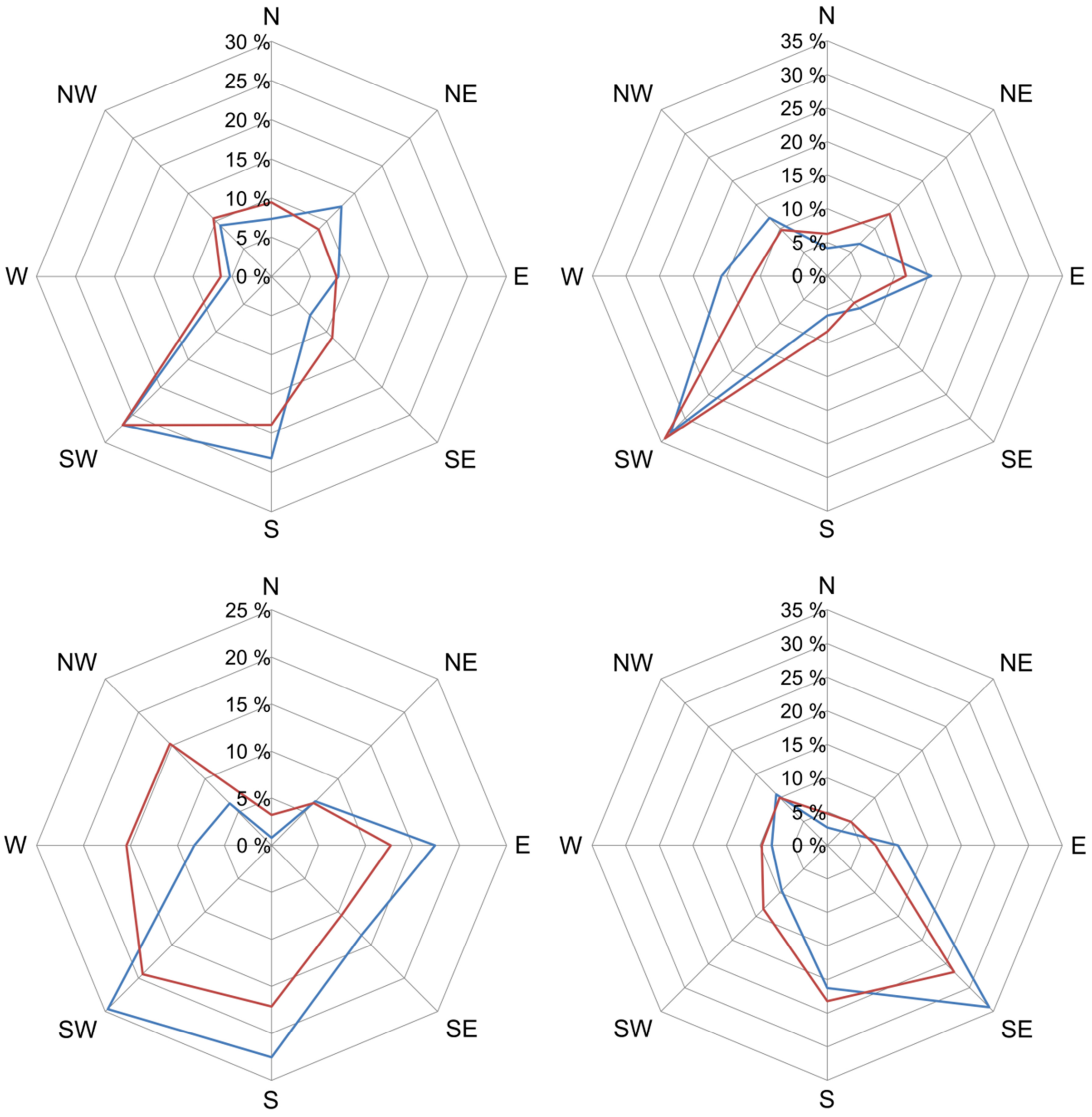


Fig. D.1 Examples for the relation between wind data recorded in 2 weeks before arthropod sampling in June/July (blue line) as used in chapters 1 and 2 and wind data sampled from June to October (red line) as used in chapter 4.

Curriculum vitae

Martin Ludwig

Personal Data

Date and place of birth	28 March 1983, Herdecke

Education

May 2011 – March 2017	PhD-Student at the Institute of Horticultural Production Systems, Department Phytomedicine, Gottfried Wilhelm Leibniz Universität Topic: “Pest prevention by functional biodiversity at *Brassica*”
Sept. 2003 – Apr. 2010	Biology (Diploma), University of Bochum and University of Göttingen, mark: „with distinction” Main subjects: animal ecology, landscape ecology, vegetation sociology, conservation Diploma thesis in the Agroecology group, title: „Nest predation in hedges and forest edges – a landscape scale experiment“
Oct. 2009	Participation in the Greek Summer School of the Society for Conservation Biology
Aug. 1993 – June 2002	Comprehensive School Werdohl

Work experience

March 2016 – June 2016	Staff, Toom Baumarkt Butzbach
May 2011 – Dec. 2015	Scientific associate, Gottfried Wilhelm Leibniz Universität
Apr. 2011 – Aug. 2011	Freelancer, Arillus gGmbH (environmental and experiential education)
May 2010 – Feb. 2011	Scientific assistant, Georg-August University Göttingen
Sept. 2002 – June 2003	Civilian service, NABU-Naturschutzstation Kranenburg e.V.

Publication list

Peer-reviewed articles

2017

Ludwig M., Schlinkert H. & Meyhöfer R. (accepted) Wind modulated landscape effects on colonisation of Brussels sprouts by insect pests and their syrphid antagonists. *Agricultural and Forest Entomology.*

2016

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2015

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Hüweler L.A., Reineke A., **Ludwig M.**, Hondelmann P. & Meyhöfer R. (2014) Welche Bedeutung hat Winterraps bei der Besiedlung von Gemüsekohl durch die Kohlmottenschildlaus: Populationsgenetische Untersuchungen mit Hilfe von Mikrosatelliten. Relevance of winter rape for colonisation of cabbage by cabbage whitefly: Studying population genetics with microsatellite markers. In: *Julius-Kühn-Archiv,* pp. 267–268. Freiburg, 23.-26.9.2014.

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Schlinkert H., Fischer C., **Ludwig M.**, Holzschuh A., Kovács A., Tscharntke T. & Batáry P. (2010) The impact of hedgerow-forest connectivity on small mammals in agricultural landscapes. In: *Verhandlungen der Gesellschaft für Ökologie,* p. 128. Giessen, 30. Aug. - 3. Sept., Vol. 40.