Effects of landscape heterogeneity and land use on interacting groups of solitary bees, wasps and their flying and ground-dwelling antagonists

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Doktorurkunde ausgehändigt am:

When the ripe pears droop heavily,
The yellow wasp hums loud and long
His hot and drowsy autumn song:
A yellow flame he seems to be,
When darting suddenly from high
He lights where fallen peaches lie.
Yellow and black – this tiny thing's
A tiger-soul on elfin wings.

'The Wasp' by William Sharp (1856 – 1905)

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel “Effects of landscape heterogeneity and land use on interacting groups of solitary bees, wasps and their flying and ground-dwelling antagonists“ selbständig, am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter der Anleitung und Betreuung durch Herrn Dr. Marcell K. Peters, Frau Dr. Catrin Westphal und Herrn Prof. Dr. Ingolf Steffan-Dewenter angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

J. Steckel

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TABLE OF CONTENTS

1 SUMMARY

Within the last decades, land use intensification reduced the heterogeneity of habitats and landscapes. The resulting pauperization led to habitats and landscapes that are spatially or temporally limited in food and nesting resources for solitary bees and wasps. Hence, biodiversity and ecosystem processes are seriously threatened. The impacts of changing resource conditions for valuable pollinators and (pest) predators remain poorly studied as well as their top-down regulation by natural enemies. Further, the reproductive success of solitary bees as response to changed resource distribution within foraging ranges is rarely examined.

We considered trap-nesting bees, wasps and their antagonists as suitable model organisms to fill these gaps of knowledge, since trap nests provide insight into otherwise hidden trophic interactions, like parasitism and predation, as well as ecological processes, like pollination and reproduction. Moreover, trap-nesting species are established as essential biodiversity indicator taxa (Tscharntke, Gathmann & Steffan-Dewenter 1998; Steffan-Dewenter & Schiele 2008; Westphal *et al.* 2008).

Thus, we first asked in **Chapter II** how the reproduction of cavity-nesting bees and wasps in grasslands depends on local management Moreover, we tested land use effects on the effectiveness of two groups of antagonists in regulating bee and wasp populations by excluding ground-dwelling antagonists. We characterized nest closure type to determine their protective function against antagonist attacks. In a highly replicated, large-scaled study, we provided 95 grassland sites in three geographic regions in Germany with 760 trap-nests. The full factorial design comprised mown and unmown plots as well as plots with and without access of ground-dwelling predators to the trap nests. The colonization of bees and wasps was unaffected by ground-dwelling antagonists. However, excluding ground-dwellers enhanced the attack rate of flying antagonists. Experimental mowing marginally affected the colonization of wasps but not attack rates. Nevertheless, both treatments – mowing and predator exclusion – significantly interacted. The exclusion of ground-dwellers on mown plots resulted in higher attack rates of flying antagonists, whereas on unmown plots this effect of ground-dweller-exclusion on the attack rate of flying antagonists was not visible. Further, attack rates were determined by nest closure material, local abundance of different nest closure types as well as closure-associated antagonist species.

In Chapter III, we studied the relative impact of local land use intensity, landscape composition and configuration on the species richness and abundance of bees, wasps and their antagonists. We analysed abundances and species numbers of hosts and their antagonists as well as parasitism rate and conducted a comprehensive landscape mapping. The digitized landscape data were the basis for further calculations of landscape metrics, like landscape composition (measured as Shannon's Diversity Index) and configuration (measured as Shape Index), within eight spatial scales ranging from 250 to 2,000 m radii. We used a compound, additive index of local land use intensity. Host abundance was only marginally negatively affected by local land use intensity. However, landscape composition at small spatial scales (250 m) enhanced the species richness and abundance of hosts, while species richness and abundance of antagonists was positively related to landscape configuration at larger spatial scales (1,500 m).

In the last study, presented in **Chapter IV**, we observed nesting bees on a selection of 18 grassland sites in two of the three research regions. We estimated the importance of resource distribution for pollen-nectar trips and consequences for the reproductive success of the solitary Red Mason Bee (*Osmia bicornis*). Local land use intensity, local flower cover as well as landscape composition and configuration were considered as critical factors of influence. We equipped each grassland site with eight trap nests and 50 female bees. Different nest building activities, like foraging trips for pollen and nectar, were measured. After the nesting season, we calculated measures of reproductive success. Foraging trips for pollen and nectar were significantly shorter in spatially complex landscapes (high Shape Index), but were neither affected by local metrics nor landscape composition (Shannon's Diversity Index and proportion of semi-natural habitats). We found no evidence that the duration of pollen-nectar trips determines the reproductive success.

To conclude, predation and parasitism of solitary bees and wasps by flying antagonists are modulated by ground-dwelling predators, local habitat management and host-specific defence strategies. Solitary bees and wasps benefitted from small-scaled landscape composition, while their flying antagonists responded to large-scaled landscape configuration. Thus, to maintain trophic interactions and biodiversity, local land use as well as landscape diversity and spatial complexity should be accounted for to create spatial and temporal stability of food and nesting resources within small spatial scales. Concrete steps to support pollinator populations include hedges, sown field margins or other linear elements. These measures that enhance the connectivity of landscapes can also support flying antagonists.

2 ZUSAMMENFASSUNG

Die Heterogenität unserer heutigen Landschaften und Habitate ist geprägt und von jahrzehntelanger Landnutzungsintensivierung. Die daraus hervorgegangene Verarmung von weiträumigen Arealen führte zu einer zeitlich und räumlich stark eingeschränkten Verfügbarkeit von Nistmöglichkeiten und Nahrungsressourcen für Wildbienen und Wespen. Die Folgen sich verändernder Ressourcenverfügbarkeit für Wildbienen und Wespen war und ist eine Gefährdung der Artenvielfalt und der Ökosystemprozesse, die diese Arten in Gang halten. Konsequenzen für diese wichtigen Bestäuber und (Pest-) Prädatoren sind kaum erforscht, genauso wenig wie für ihre Gegenspieler als natürliche Top-Down-Regulatoren. Außerdem sind die Folgen veränderter Ressourcenverfügbarkeit innerhalb der Fouragierradien von Wildbienen auf den Bruterfolg wenig untersucht.

Nisthilfen für Wildbienen, Wespen und ihre natürlichen Gegenspieler eignen sich hervorragend um diese Wissenslücken zu füllen, da sie wertvolle Einblicke gewähren in ansonsten verborgene trophische Interaktionen, wie Parasitierung und Prädation, aber auch in Ökosystemprozesse wie Bestäubung und Reproduktion. Nicht zuletzt haben sich Nisthilfen-Arten als repräsentative Biodiversitäts-Indikatoren bewährt (Tscharntke *et al.* 1998; Steffan-Dewenter & Schiele 2008; Westphal *et al.* 2008).

Somit stellten wir uns in **Kapitel II** zunächst die Frage, wie die Abundanz von stängelnistenden Bienen und Wespen im Grünland von dessen Bewirtschaftung abhängt. Außerdem untersuchten wir, wie Landnutzung die Effektivität der Top-Down-Regulation von Wildbienen und Wespen durch zwei verschiedene Gruppen von Gegenspielern (fliegende und bodenlebende) beeinflusst. Dazu haben wir einer der beiden Gruppen, den bodenlebenden Gegenspielern, den Zugang zu den Nisthilfen vorenthalten. Überdies unterschieden wir sieben verschiedene Nestverschlüsse der Liniennester um ihre Funktion als Schutz gegen natürliche Gegenspieler zu analysieren. In einer großangelegten Feldstudie, die sich über drei verschiedene Regionen Deutschlands erstreckte, installierten wir 760 Nisthilfen auf 95 Grünlandflächen. Der vollfaktorielle

Versuchsplan beinhaltete gemähte und nicht gemähte Versuchsplots, sowie Plots mit und ohne Ausschluss von Bodenprädatoren. Wildbienen und Wespen besiedelten die Nisthilfen unabhängig davon, ob Bodenprädatoren nun Zugang zu den Nisthilfen hatten oder nicht. Allerdings erhöhte sich die Rate der von fliegenden Gegenspielern gefressenen und parasitierten Brutzellen (Fressrate) sobald bodenlebende Gegenspieler ausgeschlossen wurden. Diese Fressrate war vom experimentellen Mähen unabhängig. Jedoch wiesen ungemähte Versuchsplots marginal signifikant mehr Brutzellen von Wespen auf. Beide Manipulationen, das Mähen und der Prädatorausschluss, interagierten signifikant. So wurden auf gemähten Plots, auf denen Bodenprädatoren ausgeschlossen waren, höhere Fressraten der fliegenden Gegenspieler beobachtet, während dieser Effekt auf der ungemähten Plots ausblieb. Schließlich war die Fressrate auch abhängig vom Nestverschluss, aber auch von der lokalen Häufigkeit eines jeden Verschlusses und der Anzahl an fliegenden Gegenspielern, die mit dem jeweiligen Nestverschluss assoziiert sind.

Das Thema in **Kapitel III** ist der relative Einfluss lokaler Grünlandnutzung, Landschaftsdiversität und Landschaftsstruktur auf Artenvielfalt und –abundanz von Wildbienen, Wespen und ihrer fliegenden Gegenspieler. Dazu kartierten wir Landnutzungstypen innerhalb konzentrischer Kreise um die Versuchsplots. Mithilfe der digitalisierten Landschaftsdaten berechneten wir Indices, wie den „Shannon's Diversity Index" und den „Shape Index", als Maße für Landschaftsdiversität und –struktur für acht Radien von 250 m bis 2000 m. Der negative Effekt lokaler Landnutzung auf die Wirtsabundanz war nur marginal signifikant. Jedoch stellten wir einen positiven Effekt der Landschaftsdiversität innerhalb kleiner Radien (250 m) auf die Artenvielfalt und –abundanz der Wirte fest. Die fliegenden Gegenspieler allerdings profitierten von einer komplexen Landschaftsstruktur innerhalb großer Radien von 1500 m.

Die letzte Studie, vorgestellt in **Kapitel IV**, behandelt die Bedeutung von Ressourcenverfügbarkeit für die Dauer von Fouragierflügen und die sich daraus ergebenen Konsequenzen für den Reproduktionserfolg der Roten Mauerbiene (*Osmia bicornis*). Dazu beobachteten wir nistenden Bienen auf 18 Grünlandflächen in zwei der Untersuchungsregionen in Deuschland. Wir ermittelten die lokale Landnutzungsintensität, lokale Blütendeckung sowie Landschaftsdiversität und –struktur als wichtige potentielle Einflussfaktoren. Jede Grünlandfläche wurde mit acht Nisthilfen und 50 weiblichen Bienen ausgestattet. Verschiedene Nestbau-Aktivitäten, wie Fouragierflüge für Pollen und Nektar, wurden aufgenommen. Nach Anlage der Nester ermittelten wir den Reproduktionserfolg. Wir stellten fest, dass Fouragierflüge für Pollen und Nektar in komplexen, strukturreichen Landschaften signifikant kürzer waren, dass jedoch weder lokale Faktoren, noch Landschaftsdiversität eine Rolle spielten. Wir konnten keinen Zusammenhang zwischen der Dauer von Fouragierflügen und Reproduktionserfolg feststellen.

Diese Arbeit konnte Zusammenhänge innerhalb stängelnistender Artengemeinschaften in Abhängigkeit von lokalen Landnutzungsfaktoren und verschiedenen Aspekten von Landschaftsheterogenität aufzeigen. Zusammenfassend wurde die Rate der von fliegenden Gegenspielern gefressenen und parasitierten Brutzellen reguliert durch den Ausschluss von Bodenprädatoren, lokale Landnutzung und nestspezifische Abwehrprozesse. Außerdem profitierten Wildbienen und Wespen von kleinräumiger Landschaftsdiversität, während ihre fliegenden Gegenspieler positiv auf Landschaftsstruktur innerhalb größerer Fouragierradien reagierten. Um eine räumlich und zeitlich konstante Versorgung von Nahrungs- und Nistressourcen zu gewährleisten und damit biotische Interaktionen, Diversität und Besiedlungserfolg von Wildbienen, Wespen und ihrer Gegenspieler zu unterstützen, empfehlen wir Maßnahmen, die sowohl die lokale Landnutzung als auch unterschiedliche Landschaftsfaktoren berücksichtigen. Ganz konkret empfehlen wir kleinräumige Strukturen wie Feldsäume, Ackerrandstreifen, Hecken und Korridore, die möglichst vielfältige Habitate miteinander verbinden.

3 CHAPTER I

General introduction

3.1 AGRICULTURAL INTENSIFICATION

The intensification of land use led to a reduction of biodiversity and biotic interactions at local and landscape scales (Tscharntke *et al.* 2005; Hendrickx *et al.* 2007; Holzschuh *et al.* 2007a; Karp *et al.* 2012; Socher *et al.* 2012). Meadow fauna declines as response to harvesting techniques (Humbert, Ghazoul & Walter 2009). Grassland management can either directly affect arthropod communities by the destruction of vegetation or indirectly by altering resource availability food (Steffan-Dewenter & Leschke 2003; Borer, Seabloom & Tilman 2012; Socher *et al.* 2012). Hence, pollinators suffer from intensive management reducing floral and nesting resources within a limited home range (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007; Hudewenz *et al.* 2012). A high habitat heterogeneity in turn can supply wasps with prey and bees with pollen and nectar due to a high flower diversity and abundance (Gathmann & Tscharntke 1999; Steffan-Dewenter & Leschke 2003). While intensive mowing decreases the abundance and diversity of most grassland species (Humbert *et al.* 2009), grazing maintains more plant species, a more complex vegetation structure (Schaich & Barthelmes 2012) as well as sward islets due to trampling and defoliation (Helden *et al.* 2010). Vegetation structure and management regime both contribute to the heterogeneity of a habitat (Dennis 2003; Schaich & Barthelmes 2012). Depending on the habitat heterogeneity species composition of grasslands can differ (Lassau *et al.* 2005; Batista Matos *et al.* 2013).

Moreover, responses of interacting groups to land use intensity can vary depending on how land use was measured, on group specific requirements and on the spatial scale studied (Kruess 2003; Holland, Bert & Fahrig 2004; Tscharntke *et al.* 2012). As a consequence, biotic interactions may decrease (Holt *et al.* 1999; Thies, Steffan-Dewenter & Tscharntke 2003; Rand, van Veen & Tscharntke 2012). Parasitism and predation, for instance, declined with increasing land use intensity of grasslands (Albrecht *et al.* 2007).

3.2 LANDSCAPE HETEROGENEITY

Species richness and biotic interactions at different trophic levels can also be differently affected by distinct components of landscape heterogeneity, like composition and configuration (Fig. 1) (Holzschuh, Steffan-Dewenter & Tscharntke 2010; Fahrig *et al.* 2011).

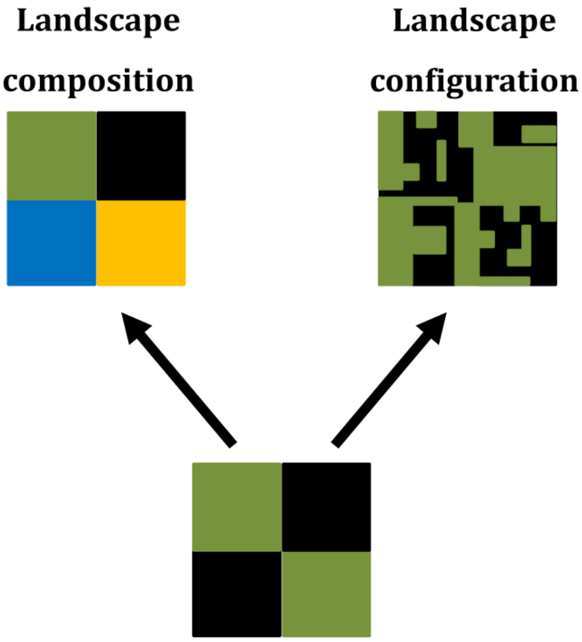

Figure 1 Difference of Landscape composition and landscape configuration starting from the same simple structured and less diverse landscape with low composition and configuration values.

Hence, landscape composition, measured as percentage of non-crop habitats, enhances bees, whereas landscape configuration, measured as edge density, facilitates wasps (Holzschuh *et al.* 2010). Parasites or parasitoids need to synchronise their habitat in space and time with host occurence (Durrer & Schmid-Hempel 1995; Steffan-Dewenter 2003). Thus, higher trophic levels are more sensitive to homogenisation of landscapes and habitat fragmentation than lower trophic levels (Holt *et al.* 1999; Chaplin-Kramer *et al.* 2011; Brueckmann *et al.* 2011; Rand *et al.* 2012). As a consequence, specialized species may be promoted in complex structured landscapes, connecting host-occupied habitats. Further, species may respond at different spatial scales depending on body size, trophic level or resource/habitat specialization. (Thies *et al.* 2003; Thies, Roschewitz & Tscharntke 2005; Tscharntke *et al.* 2005; Westphal, Steffan-Dewenter & Tscharntke 2006a; Greenleaf *et al.* 2007).

3.3 POLLINATOR POPULATIONS

The diversity of pollinating bee species declines, entailing serious consequences for their pollination of wild plants and crops (Kremen, Williams & Thorp 2002; Biesmeijer *et al.* 2006). One underlying mechanism of declines in bee populations due to land use intensification may be the efficiency of pollen-nectar foraging trips (Gathmann & Tscharntke 2002). Further drivers of bee declines, like components of landscape heterogeneity and spatial scales, have been rarely studied (Fahrig *et al.* 2011; Jha & Kremen 2013). However, species richness, abundance and reproductive success of mobile insects, like solitary bees, with varying foraging ranges, not only depend on local conditions like floral resources, but also on landscape heterogeneity and mass-flowering crops (Tylianakis *et al.* 2006; Williams & Kremen 2007; Jauker *et al.* 2012; Holzschuh *et al.* 2012). Foraging trip durations can be reduced and thereby reproductive success enhanced if food resources within home ranges are abundant (Westphal, Steffan-Dewenter & Tscharntke 2006b).

3.4 STUDY REGIONS

The study was conducted within the framework of the Biodiversity Exploratories (Fig. 2) (http://www.biodiversity-exploratories.de). This large-scale and long-term project aims to link studies that investigate land use effects on functional biodiversity and resulting consequences for ecosystem processes and taxa of different trophic levels (Fischer *et al.* 2010). The Exploratories are three research regions that span a north-south gradient within Germany, ranging from the Biosphere Reserve Schorfheide-Chorin, north of Berlin to the National Park Hainich-Dün, north of Eisenach to the Biosphere Reserve Schwäbische Alb near Münsingen (Fig. 2) (henceforth referred to as Schorfheide, Hainich and Alb). The Schorfheide in the north and the Hainich in the centre have a linear distance of 315 km; the Hainich and the Alb in the south are 319 km apart from one another.

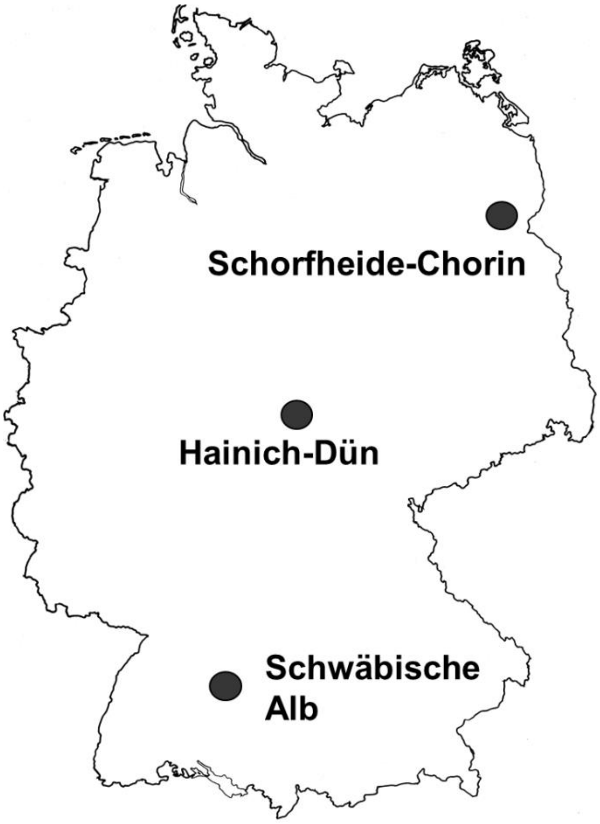

Figure 2 Location of the study regions, or so called Biodiversity Exploratories, in Germany. (figure provided by the BEO)

Typical for glacially formed lowlands comprising ground and end moraines is the Schorfheide. This exploratory covers an area of 1300 km^2. Due to this history of origin, large amounts of lakes, mires, fens and moors shape the landscape and contrast with subcontinental xerotherm grasslands on sandy hills as a result of the low annual precipitation (500-600 mm). Grasslands constitute only 6 % of the land use cover, most of the forest-free area is covered with large arable fields (32%). Altitudes range between 3 and 140 m a.s.l..

The region Hainich is dominated by deciduous forest and represents one of the largest closed forest areas in Germany. This Exploratory is of similar size as the Schorfheide with a slightly higher annual precipitation of 500 to 800 mm. The distribution of grasslands in this exploratory is less pronounced. In the face of land use change, grasslands with most fertile soils are willingly converted to arable fields. Similarly, extensive grasslands, partly on former military training sites and traditionally managed by sheep grazing, are abandoned and become overgrown or are actively reforested.

The Alb is the highest of the exploratories with 460 to 860 m a.s.l. Temperature regime is colder (6-7°C) than in the Schorfheide (8-8.5°C) and the Hainich (6.5-8°C) and annual precipitation is highest with 700 to 1000 mm. The calcareous bedrock typical for the Schwäbische Alb developed during the tertiary. Tectonic movements in the upper Rhine valley shaped characteristic calcareous mountain ranges, where dry, calcareous grasslands were managed since centuries by sheep herding. This land use type still occurs besides meadows with no or low fertilizer application and intensively used grasslands. Due to the traditional sheep herding, the landscape is mainly shaped by grasslands but is also covered by forest and mainly root crop fields. Grasslands within the former military training area Münsingen are mainly managed by sheep, a few fields are fertilized. The Biosphere Reserve covers an area of more than 45,000 ha.

3.5 STUDY DESIGN

In 2006 the project started with an extensive study of 1,000 grid plots per exploratory to analyse plant species, land use and soil conditions. Based on these data, a smaller amount of experimental plots per exploratory was chosen in 2007 to cover a broad gradient of land use intensity, ranging from semi-natural habitats to intensively used sites. These 100 experimental plots per exploratory (50 in the grassland, 50 in the forest) of 50 to 50 m were equipped with a measuring station recording air and soil temperature as well as soil humidity. The plots allow for experimental manipulations within clearly defined subplots, for instance management manipulations and the exclusion of functional groups to gain evidence about the underlying mechanisms driving land use associated functional biodiversity loss. Out of the 150 established experimental grassland plots, we chose a total of 95 plots that covered a broad land use gradient. The grassland plots differed in their type and intensity of land use by the farmers and ranged from extensive calcareous grasslands, managed by sheep herding, to intensively used pastures, grazed by cattle or horses, meadows and mown pastures (Fig 3a, b, c).

Figure 3 (a) Sheep herding at the military training area Münsingen. (b) View from a plot onto a site grazed by cattle. (c) Plot on a meadow site. (pictures by M. Bellach)

The differing management practices on the plots are recorded by annually questionnaires and interviews with land users and land owners (Fischer et al., 2010). Land use was either measured in qualitative land use categories or as a compound, additive Index (Bluethgen *et al.* 2012). A land use index enables the incorporation of the quantity of each component. Due to large differences within these components this additional information can explain much of the resulting variance in linear models. For instance, in 2008, livestock densities ranged from zero to 200 livestock units · ha^{-1}, fertilizer input from zero to 125 kg nitrogen · ha^{-1} and mowing from one to three times per year.

We used a compound, additive Land Use Index ($LUI = \left(\frac{\sum_{i-1}^{n}(y_i - y_{min})/(y_{max} - y_{min})}{n}\right) \times 100$), (Rothenwoehrer *et al.*)), which comprises grazing intensity (y_1; days grazing per year), cutting frequency (y_2; number of cuts per year) and fertilizer input (y_3; kg nitrogen per year).

3.6 STUDY SYSTEM

Cavity nesting, solitary bees offer important pollination services of wild plants and insect-pollinated crops, whereas solitary wasps are predators of (pest) insects (Fig. 4a, b) (Klein, Steffan-Dewenter & Tscharntke 2004). They can be parasitized or

Figure 4 (a) A solitary wasp providing brood cells with larvae. (b) A Red Mason Bee resting in a nest.

eaten by flying antagonists, like beetles, flies, wasps and bees. They can also be affected by ground-dwelling arthropods like earwigs, spiders and ants, acting as predators and nest displacers. Hence, sophisticated interactions between these interacting species groups can be expected. Host species within this model system rely on different habitat types within their foraging ranges that simultaneously offer food and nesting resources (Westrich 1996). Their antagonists, however, have further requirements. They depend on the distribution of hosts as well as on floral resources (Albrecht *et al.* 2007).

The model system of trap nest communities allows to study multiple trophic levels, functional groups and their biotic interactions in dependence of land use type, intensity and landscape heterogeneity.

3.7 SPECIES PORTRAIT

A very common trap-nesting bee is the Red Mason Bee *Osmia bicornis* (Synonym *O. rufa*) (Fig 3b). From March to June, this polylectic generalist constructs linear nests, made of up to 20 cells, constructed by loam. Nests are built in pre-existing cavities and sealed with loam (Westrich 1996). Brood cells of *O. bicornis* are attacked by beetle larvae of *Megatoma undata* (Linnaeus 1758), the eulophid wasp *Melittobia acasta* (Walker 1839), the specialized drosophilid fly *Cacoxenus indagator* (Loew 1858) and further antagonists (Steffan-Dewenter & Schiele 2008). *O. bicornis* relies on floral resources within 600-800 m around the nest (Gathmann & Tscharntke 2002).

3.8 CHAPTER OUTLINE AND MAIN HYPOTHESES

Despite a few studies that deal with land use effects on biodiversity and biotic interactions on local and landscape scales (Tscharntke *et al.* 2005; Hendrickx *et al.* 2007; Karp *et al.* 2012), there is still urgent need to disentangle local and landscape effects and to distinguish between different aspects of landscape heterogeneity, like composition and configuration. Species of different trophic levels respond differently to agricultural intensification, thus their interactions could fail to appear (Holt *et al.* 1999; Thies *et al.* 2003; Rand *et al.* 2012).

3.8.1 Chapter II

Therefore, we analysed biotic interactions within trap nest communities. To test the strength of biotic interactions in dependence of differently managed grasslands on interacting species groups, we manipulated the vegetation height and excluded one antagonistic group (Fig. 5a, b). Our main questions were:

I. Does the exclusion of ground-dwelling arthropods result in a higher local abundance of trap-nesting bees and wasps and a higher attack rate by flying antagonists?

II. Do solitary bees and wasps and guilds of different natural antagonists (air and ground) respond similar to manipulations of vegetation structure?

III. Are bees, wasps and their antagonists affected by vegetation structure at two spatial scales?

IV. Does the rate of attacked brood cells depend on the type of nest closure?

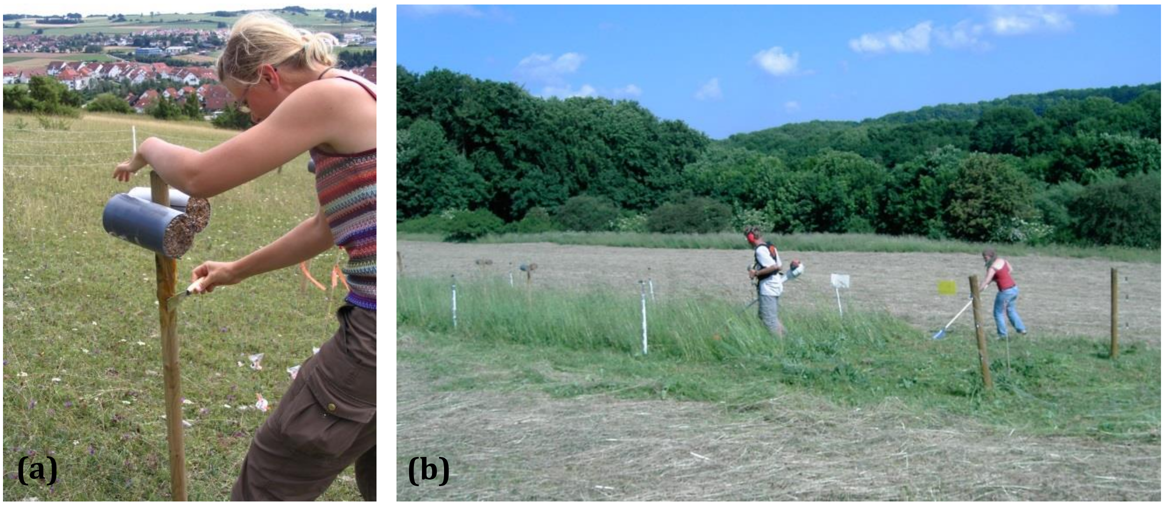

Figure 5 (a) Predator exclusion by a glue ring underneath the trap nest. (picture by M. Bellach) (b) Manipulation of the vegetation height by mowing

3.8.2 Chapter III

We investigated the relative importance of local land use intensity, landscape composition and configuration for the species richness and abundance of hosts and their antagonists. We tested the following hypothesis:

I. Species richness and abundance of hosts and their antagonists are negatively correlated with local land use intensity.
II. Hosts and antagonists are both enhanced by increasing landscape heterogeneity.
III. Hosts are stronger affected by landscape composition and antagonists by landscape configuration.
IV. Similar patterns across different geographic regions reveal the generality of landscape effects.

3.8.3 Chapter IV

We asked if the reproductive success of the cavity-nesting, solitary bee *Osmia bicornis* depends on foraging trip durations. To answer this question, we considered local land use intensity as well as landscape composition and landscape configuration as potential influencing factors in collecting food and nest building resources. Therefore, we observed several nest building activities and assessed the parasitism rate that might be reduced with shortened periods of absence from the nest. We hypothesized:

I. The duration of foraging trips affects different components of reproductive success, like (1) the number of brood cells, (2) total offspring biomass, (3) the sex ratio, (4) mortality rate, and (5) parasitism rate.
II. Longer pollen-nectar trips are compensated by reducing the time spent for other activities like partition building.

4 CHAPTER II

Habitat management mediates shifts in the impact of ground-dwelling and flying antagonists on solitary bees and wasps

Juliane Steckel, Marcell K. Peters, Catrin Westphal, Ingolf Steffan-Dewenter

(in preparation)

4.1 ABSTRACT

Agricultural intensification is a major cause of diversity loss, but consequences for top-down regulation of solitary bees and wasps are little understood. Here, we studied how local grassland management and predator exclusion affect the reproduction of above-ground nesting bees and wasps and whether attack rates by antagonists depend on nest closure type. We installed a total of 760 trap nests on 95 grassland sites in three geographical regions. To test for the combined effects of predators and habitat management, we established a full factorial experiment with mown versus unmown plots and plots with ground-dwelling predator exclusion versus control. The exclusion of ground-dwelling antagonists did not affect the colonization of bees and wasps but increased the attack rate of flying antagonists. The mowing treatments had no direct effect on reproduction and attack rates, but significantly interacted with the predator exclosure treatment. Regular management of the grassland sites explained additional variation in the abundance of bees and wasps and attack rates of flying antagonists.

Interestingly, the attack rates also depended on species specific nest closure materials, the local abundance of nest closure types and the number of associated antagonist species.

In conclusion, the top-down regulation of trap-nesting bees and wasps by flying antagonists is modified by interactions with ground-dwelling predators, local habitat management and species-specific defence strategies.

Key-Words: exclosure experiments, mowing, grazing, trophic interactions, predation, parasitism, attack rate, nest closure, trap nests

4.2 INTRODUCTION

4.2.1 Land use intensification

Negative effects of agricultural intensification on biodiversity in arable and grassland habitats are well known (Hendrickx *et al.* 2007; Karp *et al.* 2012). Grassland species may be directly affected by management through the destruction of vegetation or indirectly through a changed food supply like pollen, nectar or prey (Steffan-Dewenter & Leschke 2003). There is a general decline of meadow fauna as response to harvesting techniques, suggesting to leave uncut grass strips to preserve them (Humbert *et al.* 2009). Similarly, biotic interactions like parasitism and predation declined in intensively managed grasslands compared to restored meadows (Albrecht *et al.* 2007). Effects of management regime on spatial heterogeneity in vegetation have caused a vivid discussion with contradicting results (Adler, Raff & Lauenroth 2001). Increasing mowing frequency reduces density and diversity of most grassland groups and species (Humbert *et al.* 2009). Moreover, sward islets caused by the avoidance of dung patches, by trampling and defoliation can increase local habitat heterogeneity on grazed sites (Helden *et al.* 2010). Habitat heterogeneity can vary with respect to vegetation structure and management regime (Dennis 2003).

4.2.2 Vegetation structure & habitat heterogeneity

Vegetation structure can differently affect biotic interactions and species abundances. For instance, Auchenorrhyncha species living in higher strata were less sensitive to predation than species close to the soil (Sanders *et al.* 2008). Moreover, predators like ants and spiders only had negative effects on plant- and leafhoppers in cut, compared to uncut vegetation (Sanders *et al.* 2008). Thus, encounter frequency between prey and predators or hosts and parasitoids may be higher in cut areas or vice versa increasing vegetation structure may tend to stabilize trophic interactions and allow the coexistence of both (Gingras, Dutilleul & Boivin 2002; Brose 2003). Parasitoids and predators of above-ground nesting solitary bees and wasps, representing the highest trophic level, were most sensitive to a loss of plant species (Albrecht *et al.* 2007). Thus, food webs might be interrupted by a low sward height, while a high sward provides more resources for more species within different trophic levels and thus enhances species diversity (Lack 1969; Bazzaz 1975; Tews *et al.* 2004).

The management regime of grasslands leads to differing habitat heterogeneity (Schaich & Barthelmes 2012) and thus differing species composition, as shown for solitary wasps (Batista Matos *et al.* 2013). Invertebrate salt-marsh communities differed in their size with larger taxa dominating the un-grazed marshes and smaller taxa on cattle grazed marshes (Ford *et al.* 2013). In general, grazing compared to mowing maintains a higher spatial heterogeneity in vegetation, measured in plant species numbers, diversity indices and structural vegetation parameters such as height (Schaich & Barthelmes 2012). Mowing on the other side, can enhance blossom cover if intensity is moderate (Noordijk *et al.* 2009), whereas intensive management (mowing and fertilizing) reduces flower cover and thus has adverse effects on pollinators (Hudewenz *et al.* 2012). Bees and wasps indirectly benefit from a high habitat heterogeneity, harbouring prey for wasps or abundant and diverse flowering plants, supplying bees with pollen and nectar (Gathmann & Tscharntke 1999; Steffan-Dewenter & Leschke 2003). Similarly, unmanaged field margins or fallow strips, with higher vegetation than the field center, harbour a higher diversity and abundance of solitary bees (Holzschuh *et al.* 2010).

Flying insects might be less affected by habitat heterogeneity than ground-dwelling arthropods, that directly occupy the vegetation (Steffan-Dewenter & Tscharntke 2002; Lassau *et al.* 2005). Predacious wasps, for instance, could either benefit from sparse vegetation due to less shelter for potential prey larvae or from a diverse and abundant prey occurrence because of a multitude of niches within a high sward. Predatory species are likely to be more affected by harvesting techniques compared to their smaller prey (Humbert *et al.* 2009). Hence, effects of intensified management on biotic interactions can vary greatly, depending on the interacting groups (Warfe & Barmuta 2004).

In this study, we chose a model system comprising different groups of interacting grassland species, like above-ground nesting solitary bees as important pollinators of wild plants and insect-pollinated crops, as well as solitary wasps as predators of (pest) insects. Both of these groups are attacked by flying antagonists comprising beetles, flies, wasps and bees that act as parasites, parasitoids and predators within this system. Moreover, these hosts can be affected by ground-dwelling arthropods like earwigs, spiders and ants that directly predate offspring, feed on pollen and other food resources in brood cells, or displace nesting bees and wasps (Barthell, Frankie & Thorp 1998).

4.2.3 Trap nest system

All of these groups can be studied by so called trap nests. Communities of trap-nesting species represent a popular study system in ecology that still lacks understanding of crucial driving forces of their population dynamics (Steffan-Dewenter & Schiele 2008). Invasion of trap nests by the European earwig (*Forficula auricularia L.*) (Barthell *et al.* 1998) but also predation and parasitism due to flying antagonists in a landscape context have already been studied (Albrecht *et al.* 2007; Steffan-Dewenter & Schiele 2008). However, how both antagonist groups might interact remains unexplored (Fig. 6).

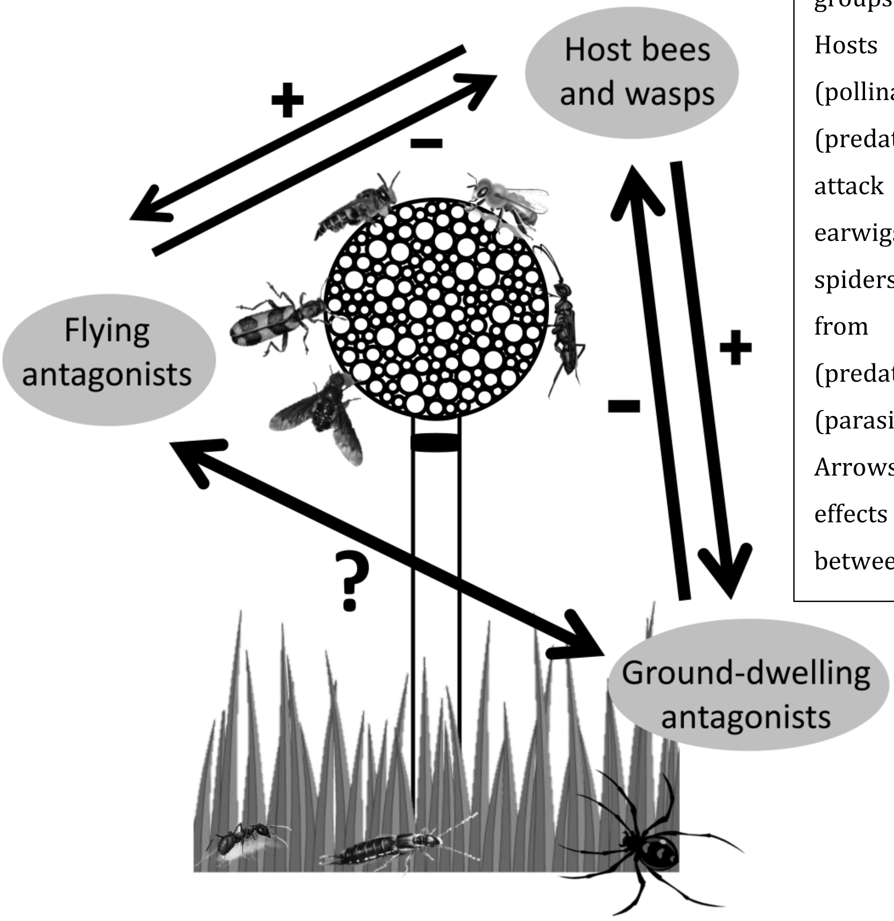

Figure 6 Interacting groups of a trap nest community. Hosts comprise solitary bees (pollinators) and solitary wasps (predators). Their antagonists attack from the ground, like earwigs (nest site displacer), spiders and ants (predators) or from the air, like beetles (predators), flies, wasps and bees (parasites and parasitoids). Arrows and signs indicate known effects of biotic interactions between the groups.

Depending on their phenology, cavity-nesting bees and wasps start to mate in spring. After fertilization, the mothers start to colonize (pre-existing) tunnels in dead wood, plants or walls (Westrich 1989). Brood cells of bees are provided with pollen and nectar before laying an egg on top of it. Wasps forage for prey like larvae, spiders or aphids to supply their offspring. After hibernation both sexes emerge and start a new population cycle. The closure of a nest, which can be constructed by loam, resin, membrane, leaf slices etc (Gathmann & Tscharntke 1999), serves as a shield against predators and parasitoids (Krombein 1967; O'Neill 2001). We expect differences in the efficiency of this shield against ground-dwelling and flying antagonists, but to our knowledge this effect has not been investigated yet.

This study explores trophic interactions across differently managed grasslands. On each grassland site, we performed a full-factorial mowing and exclosure experiment with mown versus unmown plots and predator exclosure versus control plots. While the management regime determines the habitat heterogeneity and thereby the associated species pool, small-scaled experimental manipulations of the vegetation structure can uncover the effect of vegetation structure on different interacting groups. By excluding ground-dwelling arthropods by a glue treatment, we expect a benefit for local host communities compared to the control traps without glue treatment. Our study addressed the following main questions: (1) Does the exclusion of ground-dwelling arthropods result in a higher local abundance of trap-nesting bees and wasps? (2) Does the local mowing manipulation affect solitary bees and wasps and the attack rate by flying antagonists? (3) Are bees, wasps and their antagonists affected by regular local habitat management (grazing versus mowing)? (4) Does the rate of attacked brood cells depend on the type of nest closure?

4.3 MATERIALS AND METHODS

4.3.1 Study plots and experimental design

The study was conducted on 95 grassland sites (50 x 50 m) in three different geographic regions from northeast to southwest Germany. The study regions are located within the Biosphere Reserve Schorfheide-Chorin, the National Park Hainich-Dün and the Biosphere Reserve Schwäbische Alb, henceforth referred to as

Schorfheide, Hainich and Alb, (http://www.biodiversity-exploratories.de) (Fischer *et al.* 2010) (see Appendix, Table A1). The study sites cover a gradient in local grassland management intensity.

To analyse small-scale effects of vegetation structure on biotic interactions, we established a fenced 3.5 x 14 m area on each grassland site. One half of the fenced area was mown three times (mown plot), while the other half was not managed throughout the entire season (unmown plot) (Fig. 7).

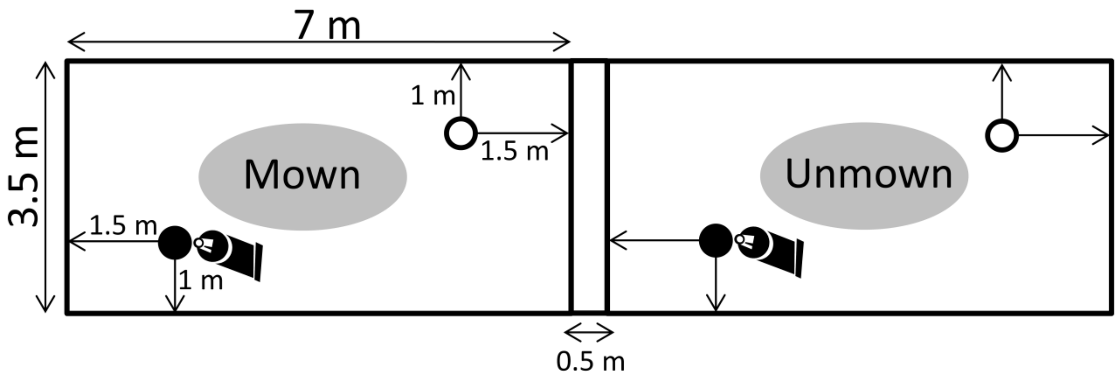

Figure 7 Study design of the two 3.5 x 7 m plots. Four wooden poles were installed, carrying two trap nests each. The illustrated configuration of the plot (the left side mown, the right unmown) varied randomly. On each half, one wooden pole was treated with a glue ring underneath the two trap nests.

On each of the two plots, two wooden poles were placed at a distance of 4 m. Two trap nests were mounted at 1.5 m height of each pole, corresponding with the maximum vegetation height. One of each pole on the mown and unmown plot was treated with a glue ring to exclude ground-dwelling arthropods from the trap nests (Fig. 7).

4.3.2 Local land use intensity

The grasslands differed in their local management and were either grazed pastures, meadows that were mown one to three times per year or grasslands that were both mown and grazed. To quantify the effect of local grassland management and of experimental treatments on resource availability, we assessed three times the flower cover in cm^2 and the floral richness on the mown and the unmown plot and on an area of 3.5 x 7 m on the surrounding grassland site.

4.3.3 Trap nest system

Trap nests represent a widely used and standardized method to sample cavity-nesting, solitary bees and wasps (Westphal *et al.* 2008). The trap nests were made of PVC tubes of 10.5 cm diameter, filled with reed internodes of different diameters (0.2 to 1.2 cm) of *Phragmites australis* (Cav.) Trin. (Gathmann, Greiler & Tscharntke 1994). 760 trap nests were installed from mid-April until mid-May 2008 and recollected at the end of September until beginning of October 2008. Trap nests were stored outside in a dry, unheated cabin to let them develop under natural conditions. During the winter month, we dissected all nests to record the number of intact, parasitized, predated or dead brood cells (Gathmann & Tscharntke 1999; Westphal *et al.* 2008). Empty nests of multivoltine species were not further analysed. We closed the nests again and stored them at room temperature to identify the hatching imagos to species level. Altogether, we quantified five response variables: (1) the total abundance, (2) the abundance of host bees and (3) the abundance of host wasps – each measured as number of brood cells per treatment combination, (4) the type of nest closure, measured as number of brood cells per closure type and treatment combination and (5) attack rate. We distinguished seven types of nest closure: membrane, leaf slices, plant particles, loam, loose loam, resin and mix (Tab. A2).

4.3.4 Statistical analyses

We used the software R 2.14.0 for Windows (R Development Core Team 2012) for statistical analyses. We constructed linear mixed models (nlme package, lme-function) to account for the hierarchical structure in the data and ln-transformed the abundances, as well as flower cover and species richness of plants to adjust for heteroscedasticity and to gain a normal distribution of the residuals. Rates have been analysed as binomial response variable by means of a generalized linear mixed model (lme4 package, lmer-function).

First, we tested if the experimental management of the plots affected the flower cover (median cm^2) and plant species richness to distinguish between direct land use effects and indirect effects of resource availability. Second, we analysed the combined effects of experimental mowing, ground-dwelling predator exclusion and their interaction with region. The grassland site was used as random effect and the plot nested within: site. Third, we performed linear mixed models with interactions of the local land use and the experimental mowing treatment to test if unmown islets served as a refuge for the tested species groups and to be able to distinguish again between disturbance effects of land use and the pure effect of vegetation structure. Fourth, we performed (generalized) linear mixed models with abundances (and rates) per pole and closure type to analyse interaction effects of glue treatment, experimental mowing treatment and closure type. Moreover, we tested if attack rates depend on closure type abundances (nests per plot) and species numbers of associated flying antagonists. Attack rates associated with closure types were compared by Tukey contrasts of multiple comparisons of means (adjusted P-values, single-step method). Model simplification was done manually by removing all non-significant terms ($P > 0.05$) (Crawley 2007).

4.4 RESULTS

A total of 22,174 brood cells were collected yielding 47 host species (23 bees, 24 wasps) and 27 flying antagonist species (22 parasitoids and three cuckoo bees, two predators). Parasitoids were found in 1,526 of the brood cells and 144 cells were attacked by predators. Altogether, 7.53 % of the brood cells were attacked by parasitoids and predators and 17.44 % died. The 22 species of parasitoids consisted of two fly and 20 wasp species. The two generalist predators were beetle larvae. Ground-dwelling arthropods like earwigs, spiders and ants either fed on offspring or displaced nesting mothers (personal observation).

4.4.1 *Effects of mowing and predator exclusion*

In contrast to our hypothesis, the exclusion of ground-dwelling arthropods did not reduce the abundance of above-ground nesting solitary bees and wasps (Tab. 1). Further, mowing treatments and interactions of mowing, predator exclusion and region had no significant effect on total brood cell numbers, and brood cell numbers of bees and wasps. Accordingly, the experimental mowing of plots neither affected flower cover ($F_{1,88}$: 0.27, P = 0.6045) nor flowering plant species richness ($F_{1,88}$: 0.52, P = 0.4729). Nevertheless, the experimental mowing treatment marginally affected wasp abundance: There were more brood cells on the unmown plot than on the mown plot (Fig. 8; $F_{1,94}$: 3.6868, P = 0.0579).

Table 1 Effects of experimental mowing (mown versus unmown plots) and predator exclusion (access of ground-dwelling as well as flying antagonists or only flying antagonists) on total host abundance (lme). (BC = brood cell number), Signif. codes: P < 0.001: ***, P < 0.01: **, P < 0.05: *

	Full model				
Sum of total BC per pole	numDF	denDF	F	P	
Intercept	1	185	838.078	< 0.001	***
Predator exclusion	1	185	1.108	0.294	
Mowing treatment	1	92	2.263	0.136	
Region	2	92	1.031	0.361	
Mowing:Predator exclusion	1	185	1.827	0.178	
Mowing:Region	2	92	0.208	0.813	

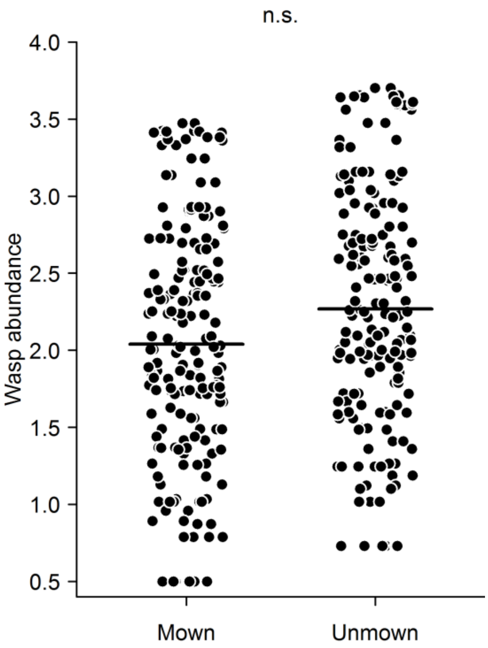

Figure 8 The experimental mowing treatment marginally affected brood cell number of wasps per pole (ln-transformed). Fitted values of the model were plotted.

The exclusion of ground-dwelling predators, but not mowing treatments ($F_{1,90} = 0.0712$, $P = 0.7902$), significantly affected attack rates of flying antagonists (Tab. 2). Interestingly, attack rates also depended on an interaction of the experimental mowing treatment and the exclusion of ground-dwellers and differed between regions (Tab. 2, Fig. 9).

Table 2 Experimental mowing effects on attack rate (lmer) with either access of ground-dwelling as well as flying antagonists or only flying antagonists. Signif. codes: $P < 0.001$: ***, $P < 0.01$: **, $P < 0.05$: *

	Full model				Final model			
Attack rate per pole	DF	χ^2	Pr ($>\chi^2$)		DF	χ^2	Pr ($>\chi^2$)	
Predator exclusion	1	14.127	< 0.001	***	1	14.135	< 0.001	***
Mowing treatment	1	0.023	0.881		1	0.024	0.876	
Region	2	16.609	< 0.001	***	2	16.640	< 0.001	***
Mowing:Predator exclusion	1	18.758	< 0.001	***	1	18.615	< 0.001	***
Mowing:Region	2	1.667	0.435		-	-	-	

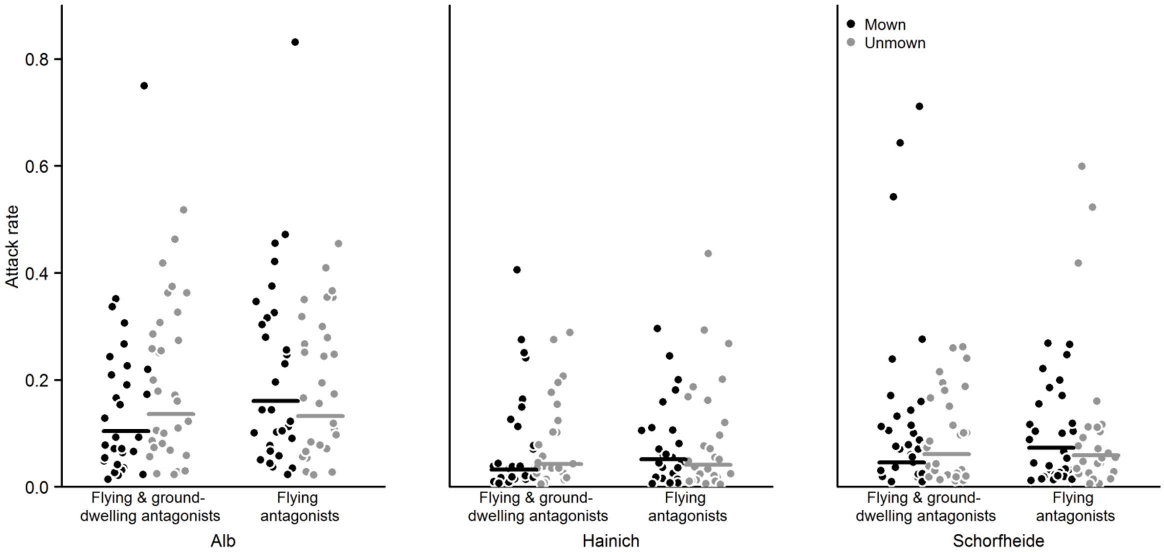

Figure 9 The attack rate of flying predators and parasitoids depended significantly on the exclusion of ground-dwellers as well as on the vegetation structure and differed between regions. Fitted values of the model were plotted.

The exclosure effect on attack rates was opposed in mown versus unmown plots. While the effect of ground-dweller-exclusion on the attack rate of flying antagonists was levelled on the unmown plots, the attack rate was higher on the mown plots when ground-dwellers were excluded. Regarding regions, highest attack rates occurred in the Alb, followed by the Schorfheide and the Hainich.

4.4.2 Effects of habitat management

In the next step we analysed how the regular local grassland management affected the abundance and antagonist interactions of bees and wasps. Although the local land use categories (grazed, mown and grazed & mown) did not affect flower cover ($F_{1,53}$: 1.279, P = 0.2632) total host abundance was affected by local land use categories (Fig. 10, Tab. 3). The highest abundance of bees and wasps occurred on the grazed sites and differed significantly from the mown sites (P < 0.01, Fig. 10).

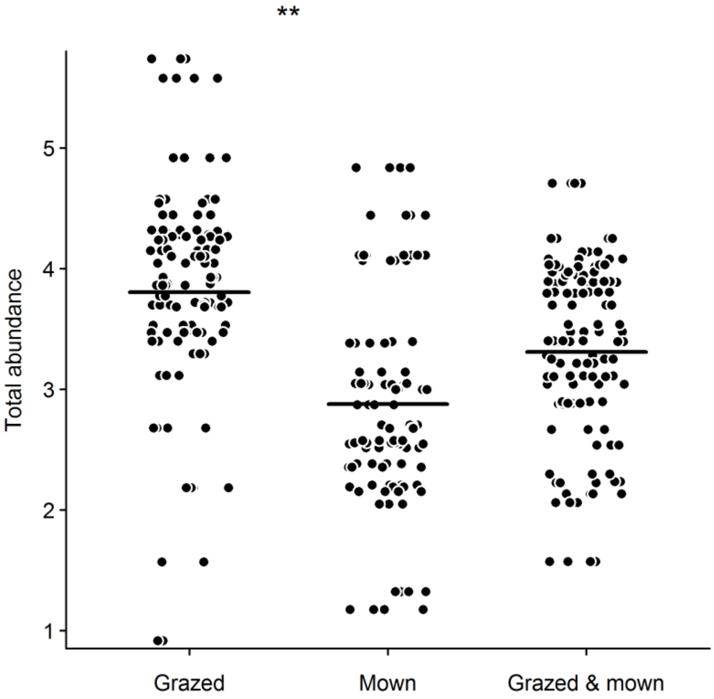

Figure 10 Sum of total brood cells per pole (ln-transformed) was significantly lower on the mown compared to the grazed plots. Significance was evaluated by Tukey contrasts of multiple comparisons of means (adjusted P-values, single-step method). Fitted values of the model were plotted.

Table 3 (Generalized) linear mixed effect models testing for interaction effects of experimental mowing treatment and local land use of the grassland site. Abundances were ln-transformed.

	Full model				**Final model**			
Total abundance	numDF	denDF	F	P	numDF	denDF	F	P
Intercept	1	183	906.501	< 0.001 ***	1	187	906.776	< 0.001 ***
Predator exclusion	1	183	1.099	0.296	-	-	-	-
Mowing treatment	1	92	2.260	0.136	-	-	-	-
Land use regime	2	90	5.324	0.007 **	2	90	5.323	0.007 **
Predator exclusion:Mowing	1	183	1.801	0.181	-	-	-	-
Predator exclusion:Land use regime	2	183	0.187	0.830	-	-	-	-
Mowing:Land use regime	2	92	0.040	0.961	-	-	-	-
Bee abundance	numDF	denDF	F	P	numDF	denDF	F	P
Intercept	1	183	445.843	< 0.001 ***	1	282	445.682	< 0.001 ***
Predator exclusion	1	183	1.954	0.164	-	-	-	-
Mowing treatment	1	92	1.318	0.254	-	-	-	-
Land use regime	2	90	3.215	0.045 *	2	90	3.215	0.045 *
Predator exclusion:Mowing	1	183	0.887	0.348	-	-	-	-
Predator exclusion:Land use regime	2	183	0.222	0.801	-	-	-	-
Mowing:Land use regime	2	92	0.025	0.975	-	-	-	-
Wasp abundance	numDF	denDF	F	P	numDF	denDF	F	P
Intercept	1	184	401.205	< 0.001 ***	1	188	410.790	< 0.001 ***
Predator exclusion	1	184	0.148	0.701	-	-	-	-
Mowing treatment	1	92	3.677	0.058	-	-	-	-
Land use regime	2	90	4.531	0.013 *	2	90	4.643	0.012 *
Predator exclusion:Mowing	1	184	2.696	0.102	-	-	-	-
Predator exclusion:Land use regime	2	184	0.704	0.496	-	-	-	-
Mowing:Land use regime	2	92	0.006	0.994	-	-	-	-
Attack rate		DF	χ^2	Pr ($>\chi^2$)		DF	χ^2	Pr ($>\chi^2$)
Predator exclusion		1	14.123	< 0.001 ***		1	14.147	< 0.001 ***
Mowing treatment		1	0.016	0.900		1	0.015	0.902
Land use regime		2	0.125	0.939		2	0.120	0.942
Predator exclusion:Mowing		1	19.257	< 0.001 ***		1	18.575	< 0.001 ***
Predator exclusion:Land use regime		2	1.818	0.403		-	-	-
Mowing:Land use regime		2	10.606	0.005 **		2	10.323	0.006 **

Interestingly, attack rates were not only affected by the experimental mowing and predator exclusion, but depended also on the surrounding land use (Fig. 11, Tab. 3). Attack rates were highest, when ground-dwelling arthropods were excluded (Tab. 3) and lowest on mown control plots (no predator exclusion) within mown grassland sites (Fig. 11). Concurrently, no differences in the attack rate between experimental mowing treatments were revealed on exclosure treatments on mown grasslands (Fig. 11).

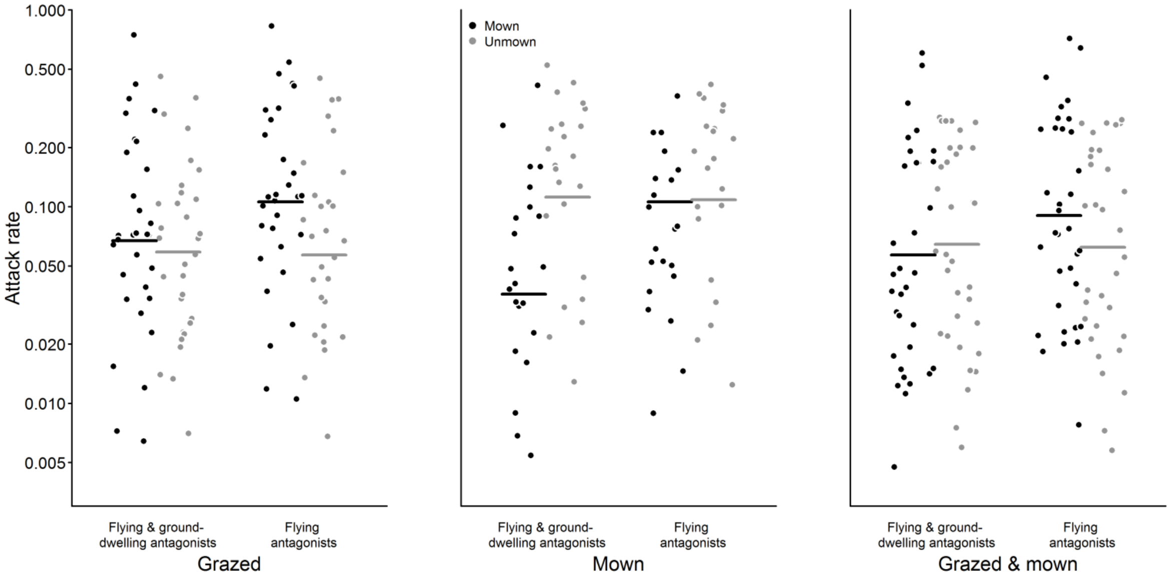

Figure 11 The attack rate of flying antagonists depended on the access of ground-dwellers, which affected flying antagonists differently depending on the vegetation structure. The attack rate also depended on an interaction of vegetation structure with grassland management regime. Fitted values of the model were plotted.

4.4.3 Effects of closure type as a protection against antagonists

We analysed if the type of nest closure would contribute to explain the number of nests and the amount of brood cells attacked by flying antagonists, beside the exclusion of ground-dwelling arthropods and the experimental mowing treatment. Number of brood cells differed significantly between closure types (Tab. 4). Each closure type was associated with different antagonist species and abundances (Tab. A3). The closure type which was least attacked by flying antagonists was 'membrane', followed by 'loose loam', 'mix' and 'loam', then 'resin', 'plant particles' and 'leaf slices', which was most attacked (Fig. 12, Tab. A4). Interestingly, the attack rate significantly decreased with increasing closure type abundances and tended to increase with increasing numbers of antagonist species (Tab. 5). Similarly, increasing closure type abundances enhanced the number of antagonist species ($F_{1,56}$: 5.04, $P < 0.05$).

Table 4 Effects of local treatment combinations and nest closure types on the sum of total, bee and wasp abundance (brood cells) and on the attack rates per pole. Signif. codes: P < 0.001: ***, P < 0.01: **, P < 0.05: *

	Full model					**Final model**				
Total abundance	numDF	denDF	F	P		numDF	denDF	F	P	
Intercept	1	377	1621.695	< 0.001	***	1	389	1426.851	< 0.001	***
Mowing treatment	1	85	1.027	0.314		-	-	-	-	
Predator exclusion	1	141	1.591	0.209		-	-	-	-	
Closure	6	377	22.646	< 0.001	***	6	389	22.735	< 0.001	***
Mowing:Predator exclusion	1	141	0.000	0.999		-	-	-	-	
Mowing:Closure	6	377	0.862	0.523		-	-	-	-	
Predator exclusion:Closure	6	377	0.149	0.989		-	-	-	-	
Bee abundance	numDF	denDF	F	P		numDF	denDF	F	P	
Intercept	1	202	768.310	< 0.001	***	1	212	651.798	< 0.001	***
Mowing treatment	1	79	0.856	0.358		-	-	-	-	
Predator exclusion	1	123	2.148	0.145		-	-	-	-	
Closure	5	202	23.550	< 0.001	***	5	212	23.544	< 0.001	***
Mowing:Predator exclusion	1	123	0.030	0.862		-	-	-	-	
Mowing:Closure	5	202	0.268	0.930		-	-	-	-	
Predator exclusion:Closure	5	202	0.590	0.707		-	-	-	-	
Wasp abundance	numDF	denDF	F	P		numDF	denDF	F	P	
Intercept	1	74	633.937	< 0.001	***	-	-	-	-	
Mowing treatment	1	48	0.198	0.658		-	-	-	-	
Predator exclusion	1	57	0.388	0.536		-	-	-	-	
Closure	4	27	1.859	0.147		-	-	-	-	
Mowing:Closure	4	27	1.244	0.316		-	-	-	-	
Attack rate		DF	χ^2	Pr (>χ^2)			DF	χ^2	Pr (>χ^2)	
Mowing treatment		2	4.733	0.094			1	2.701	0.100	
Predator exclusion		1	2.670	0.102			1	2.615	0.106	
Closure		8	178.878	< 0.001	***		6	205.404	< 0.001	***
Mowing:Predator exclusion		1	3.689	0.055			1	3.889	0.049	*
Mowing:Closure		6	4.047	0.670			-	-	-	
Predator exclusion:Closure		6	7.938	0.243			-	-	-	

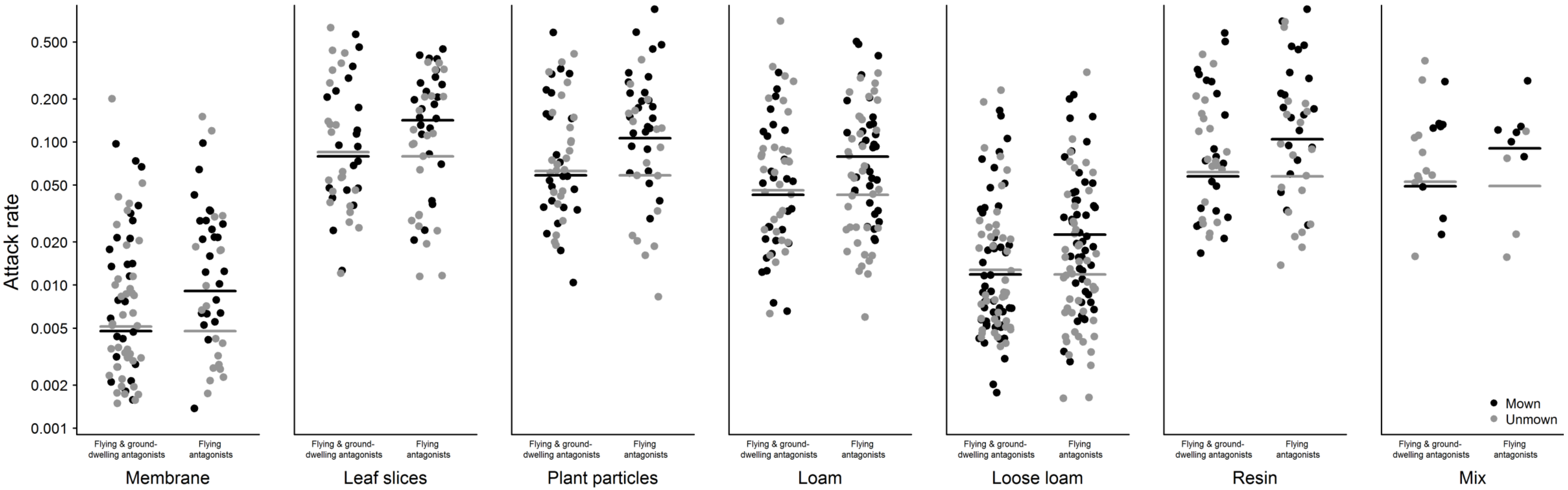

Figure 12 The attack rate of flying antagonists varied significantly between different nest closure types and showed reverse effects of experimental mowing on poles where predators were excluded and on poles where predators had access. Fitted values of the model were plotted. For model estimates see Tab. A5.

Again, attack rates were significantly reduced on mown plots when ground-dwelling arthropods had access (Fig. 12, Tab. 4).

Table 5 Analysis of deviance and estimates of a lmer analysing the dependence of attack rates on closure type abundances (nests per plot) and species numbers of associated flying antagonists. Signif. codes: P < 0.001: ***, P < 0.01: **, P < 0.05: *

Attack rate	DF	χ^2	Pr ($>\chi^2$)	
Closure type abundance	1	12.083	< 0.001	***
Species richness of antagonists	1	3.067	0.080	
Closure type	6	19.481	0.003	**

	Estimate	SE	z	P	
Membrane	0.068	0.540	-4.858	< 0.001	***
Leaf slices	0.177	0.561	1.935	0.053	
Loam	0.127	0.560	1.245	0.213	
Loose loam	0.053	0.579	-0.466	0.641	
Mix	0.196	0.791	1.528	0.127	
Plant particles	0.161	0.581	1.677	0.093	
Resin	0.167	0.598	1.699	0.089	
Closure type abundance	-0.011	0.003	-3.476	< 0.001	***
Species richness of antagonists	0.255	0.146	1.751	0.080	

4.5 DISCUSSION

In this study, we could experimentally evaluate how the relative impact of flying and ground-dwelling antagonists on a community of solitary bees and wasps is modulated by local habitat management. We could show that ground-dwelling arthropods did not directly reduce the brood cell numbers of above-ground-nesting solitary bees and wasps but their exclusion changed attack rates of flying antagonists. Vegetation structure on unmown plots equally reduced the effectiveness of both antagonistic groups. Host bees and wasps in contrast were marginally enhanced on unmown plots with high vegetation. Local habitat management like grazing presumably caused more habitat heterogeneity than mowing and thereby also enhanced host abundance and similarly reduced the effectiveness of both antagonistic groups. Finally, we found trait-specific differences in the precedence of being attacked by considering the closure type of a nest.

Our results provide no evidence for a direct negative effect of ground-dwelling arthropods on the local abundance of trap-nesting bees and wasps. Nevertheless, ground-dwellers significantly affected the attack rates by flying antagonists on mown plots with low vegetation height. On control poles (no exclusion of ground-dwellers), attack rates consistently decreased (Fig. 9, Fig. 11, Fig. 12), but depended on the experimental mowing treatment. We speculate that the presence of ground-dwellers is causing an avoidance behaviour of nests by flying antagonists. The mechanism underlying the displacement of flying antagonists might be regulated by extrinsic information gathered visually or chemically (Dicke & Grostal 2001).

Abundances of host bees and wasps were only affected by the surrounding land use regime and less sensitive to small-scaled manipulations of vegetation structure. Grazed sites enhanced the colonization of bees and wasps, compared to mown sites. Moreover, less host brood cells were attacked by flying antagonists (predator exclusion) on plots where the surrounding grassland sites were either grazed or mown and grazed. We assume that high vegetation offers a visual shelter against flying antagonists and therefore dampened their attack rate. Antagonistic interactions were most pronounced on mown plots with low vegetation structure within a mown surrounding, where habitat heterogeneity was assumed to be lowest. This corresponds to studies that proclaim a higher encounter rate between prey and predators or hosts and parasitoids in mown areas (Gingras *et al.* 2002; Sanders *et al.* 2008). The involved group of ground-dwelling arthropods does not exclusively depend on above-ground nesting bees and wasps or their nesting sites, but rather depends on prey items within the vegetation. Accordingly, the high vegetation on unmown plots completely levelled out the antagonistic effects of ground-dwellers on mown grassland sites (Fig. 11). This interaction effect was not visible on grazed or grazed & mown sites, where higher habitat heterogeneity might have handicapped both – flying and ground-dwelling antagonists. To conclude, structurally complex vegetation modulated biotic interactions between flying and ground-dwelling antagonists of bees and wasps.

The type of nest closure might determine how easily a predator, parasite or parasitoid can enter the nest after it has been closed. We found differences in the attack rate of flying antagonists between closure types. Attack rates were lowest in nests protected by a thin membrane and highest in nests closed by leaf slices. More solid materials like loam and resin did not guarantee a better protection, because attack rates were also negatively related to the abundance of a nest closure type: Attack rates differed between closure types and decreased with increasing local abundance of a certain closure type (Tab. 5). Aggregation of nests may improve host defence against antagonists by parasite confusion, active group defence or improved parasite detection (Rosenheim 1990). For instance differing attack rates between leaf-slice and loose-loam nests could be a combined result of local closure type abundance, the closure type itself and the associated number of antagonist species, which was equal in this case (seven) (Tab. A3). In comparison to loose-loam nests, leaf-slice nests may be easier to burst but much less abundant (cf. Tab. A3).

4.6 CONCLUSIONS

Communities of solitary bees and wasps are regulated by different factors: local land use, type of nest closure, flying and ground-dwelling antagonists and most do interact. A land use regime that increased habitat heterogeneity enhanced the abundance of above-ground nesting solitary bees and wasps. Small-scaled experimental manipulations of the vegetation structure uncovered the susceptibility of biotic interactions between hosts and their ground-dwelling and flying antagonists: Hosts nesting in high vegetation were protected from being attacked by both antagonistic groups, whereas on low vegetation sites ground-dwelling arthropods reduced the attack rate of flying antagonists. Thus, these interacting groups are differently affected by habitat heterogeneity. This knowledge can help to estimate the efficiency of agri-environment schemes such as fallow strips or sward islets within differently managed grasslands. To preserve these reticulate interactions within trap nest communities a mixture of habitats differing in vegetation structure are recommended. Moreover, factors determining the effectiveness of nest closure types in protecting the nest were unknown so far and offer valuable insight into possible evolutionary adaptations. For instance, even less solid nest closures like membrane do not necessarily imply a disadvantage if these nests are locally aggregated and only attacked by few different antagonist species.

To conclude, our findings imply that small scale and local habitat management affect top-down regulation of bee and wasp populations through changes in the interactions between ground-dwelling and flying antagonists.

4.7 APPENDIX

Table A1 (part 1) Coordinates of the plots in 2008

Plot	Longitude	Latitude
AEG01	9.341986753	48.39800501
AEG02	9.472784124	48.37685727
AEG03	9.532378750	48.40888149
AEG04	9.418889124	48.38088846
AEG05	9.439200708	48.39587587
AEG06	9.441678107	48.40126215
AEG07	9.376847130	48.39142098
AEG08	9.492124587	48.42264029
AEG09	9.502792380	48.39467093
AEG10	9.267689544	48.39370579
AEG11	9.347715524	48.48539880
AEG12	9.350230928	48.38912209
AEG13	9.362198270	48.39164797
AEG18	9.521442437	48.38294187
AEG19	9.447318583	48.39764314
AEG20	9.356402081	48.48950889
AEG21	9.357219301	48.44220388
AEG22	9.513423041	48.40438132
AEG25	9.259596583	48.39547800
AEG26	9.403881830	48.39510617
AEG27	9.479931659	48.41913964
AEG32	9.485781341	48.46583327
AEG33	9.491051148	48.45142224
AEG34	9.500558067	48.45587769
AEG36	9.299243825	48.47816117
AEG37	9.413545473	48.39615094
AEG38	9.425251134	48.43954414
AEG39	9.425682926	48.39421808
AEG41	9.398486134	48.36994461
AEG42	9.376017925	48.39798857
AEG46	9.434888800	48.39697142
AEG47	9.446157209	48.41923078
AEG48	9.498669675	48.42184768
HEG01	10.405345410	50.97164464
HEG02	10.429992880	51.00074516
HEG03	10.432931720	50.99808772
HEG04	10.436164530	51.11335874
HEG05	10.322511860	51.21589148
HEG06	10.391206110	51.21493181
HEG07	10.410398510	51.27357932
HEG08	10.417930500	51.27125420
HEG09	10.380772620	51.22389419
HEG11	10.456164020	51.28066363
HEG17	10.470439780	51.07050072
HEG19	10.473203550	51.07323367
HEG21	10.752554210	51.19069944
HEG24	10.351198440	51.10106312
HEG26	10.371711220	51.28149786
HEG27	10.596972740	51.08644290
HEG29	10.498413220	51.26410639
HEG30	10.359895890	51.20184935
HEG33	10.425947280	51.11143283
HEG34	10.386920390	51.21428854
HEG36	10.510216770	51.03144248
HEG37	10.514477700	51.03238665
HEG39	10.346231760	51.12022161
HEG40	10.446796600	50.96680908
HEG43	10.435804110	51.30196760
HEG46	10.753533900	51.20689018
HEG47	10.371902500	51.28419730
HEG49	10.391868990	51.27889974

Table A1 (part 2) Coordinates of the plots in 2008

Plot	Longitude	Latitude
SEG01	13.969656200	53.08740378
SEG02	13.980059640	53.08929052
SEG03	13.985712430	53.10281792
SEG04	14.001884050	53.11373775
SEG05	14.000536530	53.10743621
SEG06	13.622845680	53.10348052
SEG07	13.977081330	53.08836637
SEG08	14.017112610	53.11395417
SEG09	13.612579180	53.09816722
SEG10	13.997569370	53.10660254
SEG11	13.992979240	53.10557538
SEG12	13.965179190	53.08737397
SEG14	13.980272520	53.08659650
SEG23	14.025917220	53.10764636
SEG24	13.996093380	53.09302113
SEG25	13.618003250	53.11061357
SEG28	14.006092960	53.09310496
SEG29	13.998708010	53.09034729
SEG30	13.830693620	53.14812566
SEG31	13.835451100	53.14907085
SEG32	13.832100580	53.15191364
SEG33	13.842524160	52.98576954
SEG34	13.847210810	52.98311912
SEG35	13.848329220	52.98025431
SEG36	13.837654570	52.98689030
SEG37	13.876043520	53.13491197
SEG40	13.840684020	53.11568433
SEG41	13.852355260	53.12217749
SEG44	13.965199850	52.88004268
SEG45	13.959402950	52.88143890
SEG46	13.826343190	52.97842194
SEG47	13.827593260	52.98724991
SEG48	13.606653650	53.09719043
SEG49	13.856589720	52.97471748

Table A2 (part 1) Classification of host species to nest closure types. We used the simplified closure notations.

Genus or species	**Closure simplified**	**Closure detailed**
Hylaeus	membrane	membrane
Hylaeus angustatus (Schenck)	membrane	membrane
Hylaeus communis (Nylander)	membrane	membrane
Hylaeus confusus (Nylander)	membrane	membrane
Hylaeus difformis (Eversmann)	membrane	membrane
Megachile alpicola (Alfken)	leaf slices	leaf slices, plant duff
Megachile centuncularis (Linnaeus)	leaf slices	leaf slices
Megachile versicolor (Smith)	leaf slices	leaf slices, plant duff
Anthophora furcata (Panzer)	plant particles	wood particles
Discoelius	plant particles	plant duff
Discoelius doufourii (Lepeletier)	plant particles	plant duff
Osmia caerulescens (Linnaeus)	plant particles	plant duff
Osmia claviventris (Thomson)	plant particles	plant duff
Osmia gallarum (Spinola)	plant particles	plant duff
Osmia leaiana (Kirby)	plant particles	plant duff
Osmia leucomelana (Kirby)	plant particles	plant duff
Osmia mustelina (Gerstaecker)	plant particles	plant duff
Osmia parietina (Curtis)	plant particles	plant duff
Ancistrocerus antilope (Panzer)	loam	sand, earth, loam, no stones
Ancistrocerus claripennis (Thomson)	loam	sand, earth, loam, no stones
Ancistrocerus gazella (Panzer)	loam	sand, earth, loam, no stones
Ancistrocerus nigricornis (Curtis)	loam	sand, earth, loam, no stones
Ancistrocerus parietinus (Linnaeus)	loam	sand, earth, loam, no stones
Ancistrocerus trifasciatus (Müller)	loam	sand, earth, loam, no stones
Chelostoma florisomne (Linnaeus)	loam	hard sand, earth, loam, stones
Chelostoma rapunculi (Lepeletier)	loam	hard sand, earth, loam, stones
Euodynerus quadrifasciatus (Fabricius)	loam	hard sand, earth, loam, no stones
Symmorphus angustatus (Zetterstedt)	loam	sand, earth, loam, no stones
Trypoxylon figulus (Linnaeus)	loam	sand, earth, hard loam, no stones
Chelostoma distinctum (Stoeckhert)	loose loam	soft sand, earth, loam, no stones
Gymnomerus laevipes (Shuckard)	loose loam	sand, earth, loose loam, no stones
Megachile ericetorum (Lepeletier)	loose loam	sand, earth, loose loam, no stones
Osmia bicornis (Linnaeus)	loose loam	loose loam, no stones

Table A2 (part 2) Classification of host species to nest closure types. We used the simplified closure notations.

Genus or species	Closure simplified	Closure detailed
Heriades	resin	resin
Heriades truncorum (Linnaeus)	resin	resin
Passaloecus	resin	resin
Passaloecus borealis (Dahlbom)	resin	resin plug, particles of wood and stem
Passaloecus corniger (Shuckard)	resin	resin
Passaloecus eremita (Kohl)	resin	resin
Passaloecus gracilis (Curtis)	resin	resin
Passaloecus insignis (Vander Linden)	resin	resin
Crossocerus barbipes (Dahlbom)	mix	loam, wooden duff, stem core
Dipogon bifasciatus (Geoffroy)	mix	resin, weave, sand, stones, wooden duff, plant material
Pemphredon lugens (Dahlbom)	mix	resin, sand, stones, wooden duff, plant material
Pemphredon morio (Vander Linden)	mix	stem core, wood particles
Pemphredon rugifera (Dahlbom)	mix	stem core, weave
Symmorphus allobrogus (Saussure)	mix	particles of wood, then loam
Symmorphus gracilis (Brullé)	mix	particles of wood, then loam
Symmorphus murarius (Linnaeus)	mix	particles of wood, then loam

Table A3 (part 1) Overview of the nest closure types and their associated antagonists

Closure type	No. of vital BC	Mortality rate [%]	Antagonist	No. of consumed BC	Consumption rate [%]
Membrane	618	34.19	*Gasteruption assectator (Linnaeus)*	1	2.27
			Gasteruption jaculator (Linnaeus)	5	
			Melittobia acasta (Walker)	7	
			Trichodes apiarius (Linnaeus)	1	
Leaf slices	757	22.36	*Anthrax anthrax (Schrank)*	1	14.00
			Coelioxys inermis (Kirby)	68	
			Coelioxys mandibularis (Nylander)	7	
			Ephialtes manifestator (Linnaeus)	11	
			Melittobia acasta (Walker)	15	
			Stelis phaeoptera (Kirby)	3	
			Trichodes apiarius (Linnaeus)	1	
Plant particles	1245	34.71	*Anthrax anthrax (Schrank)*	9	13.25
			Cacoxenus indagator (Loew)	1	
			Chrysidinae	4	
			Chrysura radians (Harris)	62	
			Megatoma undata (Linnaeus)	1	
			Melittobia acasta (Walker)	59	
			Sapyga quinquepunctata (Fabr.)	20	
			Stelis phaeoptera (Kirby)	1	
			Trichodes apiarius (Linnaeus)	8	

Table A3 (part 2) Overview of the nest closure types and their associated antagonists

Closure type	No. of vital BC	Mortality rate [%]	Antagonist	No. of consumed BC	Consumption rate [%]
Loam	1524	24.93	*Anthrax anthrax (Schrank)*	1	6.89
			Chrysidinae	8	
			Chrysis	2	
			Chrysis graelsii (Guérin)	4	
			Chrysis ignita B-Gruppe	14	
			Chrysis iris (Christ)	3	
			Chrysis pseudobrevitarsis (Lins.)	6	
			Chrysis solida (Haupt)	4	
			Dusona juvenilis (Forster)	1	
			Ephialtes manifestator (Linnaeus)	14	
			Melittobia acasta (Walker)	35	
			Trichrysis cyanea (Linnaeus)	13	
Loose loam	8421	12.15	*Anthrax anthrax (Schrank)*	7	3.03
			Cacoxenus indagator (Loew)	216	
			Chalcidoidea	4	
			Ephialtes manifestator (Linnaeus)	1	
			Megatoma undata (Linnaeus)	8	
			Melittobia acasta (Walker)	17	
			Trichodes apiarius (Linnaeus)	2	
Resin	820	25.66	*Chrysidinae*	39	22.07
			Ephialtes manifestator (Linnaeus)	4	
			Megatoma undata (Linnaeus)	2	
			Melittobia acasta (Walker)	57	
			Omalus	1	
			Omalus aeneus (Fabricius)	32	
			Poemenia collaris (Haupt)	1	
			Poemenia notata (Holmgren)	9	
			Pseudomalus auratus (Linnaeus)	33	
			Trichrysis cyanea (Linnaeus)	3	
Mix	155	28.24	*Chrysidinae*	3	13.55
			Chrysis ignita B-Gruppe	3	
			Ephialtes manifestator (Linnaeus)	1	
			Ephialtes zirnitsi (Ozols)	3	
			Perithous scurra (Panzer)	1	
			Pseudomalus auratus (Linnaeus)	10	

Table A4 Generalized linear mixed model of the attack rate per pole versus closure type. Tukey contrasts of multiple comparisons of means (adjusted P-values reported, single-step method)

	Estimate	SE	z	P	
Leaf slices - membrane	2.891	0.356	8.125	< 0.001	***
Loam - membrane	2.233	0.344	6.500	< 0.001	***
Loose loam - membrane	0.918	0.340	2.701	0.089	
Mix - membrane	2.379	0.429	5.543	< 0.001	***
Plant particles - membrane	2.561	0.343	7.473	< 0.001	***
Resin - membrane	2.543	0.340	7.484	< 0.001	***
Loam - leaf slices	-0.658	0.201	-3.272	0.016	*
Loose loam - leaf slices	-1.973	0.183	-10.806	< 0.001	***
Mix - leaf slices	-0.511	0.337	-1.519	0.713	
Plant particles - leaf slices	-0.329	0.218	-1.509	0.719	
Resin - leaf slices	-0.347	0.226	-1.538	0.701	
Loose loam - loam	-1.315	0.170	-7.722	< 0.001	***
Mix - loam	0.146	0.322	0.454	0.999	
Plant particles - loam	0.329	0.190	1.730	0.572	
Resin - loam	0.310	0.209	1.486	0.734	
Mix - loose loam	1.461	0.321	4.558	< 0.001	***
Plant particles - loose loam	1.643	0.188	8.739	< 0.001	***
Resin - loose loam	1.625	0.202	8.063	< 0.001	***
Plant particles - mix	0.182	0.298	0.613	0.996	
Resin - mix	0.164	0.314	0.523	0.998	
Resin - plant particles	-0.018	0.186	-0.098	1.000	

Table A5 Generalized linear mixed effect models testing for interaction effects of closure type, experimental mowing treatment and predator exclusion on the attack rate per pole. (Estimates are plotted in Fig. 7)

	Estimate	SE	z	P	
Membrane (mown, predator access)	0.005	0.418	-12.781	< 0.001	***
Leaf slices (mown, predator access)	0.079	0.356	8.125	< 0.001	***
Plant particles (mown, predator access)	0.058	0.343	7.473	< 0.001	***
Loam (mown, predator access)	0.043	0.344	6.500	< 0.001	***
Loose loam (mown, predator access)	0.012	0.340	2.701	0.007	**
Resin (mown, predator access)	0.057	0.340	7.484	< 0.001	***
Mix (mown, predator access)	0.049	0.429	5.543	< 0.001	***
Unmown	0.519	0.263	0.285	0.775	
Predator excluded	0.657	0.257	2.538	0.011	*
Unmown:Predator excluded	0.326	0.367	-1.972	0.049	*

5 CHAPTER III

Landscape composition and configuration differently affect trap-nesting bee and wasp hosts and their antagonists

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(in preparation)

5.1 ABSTRACT

Intensification of agriculture reduces heterogeneity at local and landscape scales and thereby biodiversity and ecosystem processes. We studied a host-antagonist system of cavity-nesting bees, wasps and their antagonists and hypothesized that hosts and antagonists show different responses to local land use intensity, landscape composition, landscape configuration and spatial scales.

In a highly replicated study, we established nesting resources on 95 grasslands across three geographic regions in Germany and measured the species richness and abundance of hosts (bees and wasps) and their antagonists, and rates of parasitism. For each grassland site, we quantified local land use intensity as well as landscape composition and configuration at spatial scales from 250 to 2,000 m.

Increasing landscape heterogeneity enhanced species richness, abundance and parasitism rate, whereas local land use intensity only marginally negatively affected host abundance. Interestingly, host richness and abundance were enhanced by landscape composition at small spatial scales, whereas their antagonists responded to landscape configuration at larger spatial scales.

In conclusion, landscape composition and configuration affect trophic levels differently and are more relevant for conservation schemes than local land use intensity. Solitary bees and wasps, which offer important pollination and pest control services, could be supported by enhancing landscape diversity, while population control by their antagonists could benefit from measures that promote landscape connectivity. Hence, scale-dependent and trophic group specific management schemes are required, that address different components of landscape heterogeneity to enhance functional diversity and trophic interactions in agricultural landscapes.

***Key-Words*:** Agricultural intensification, landscape heterogeneity, trophic interactions, ecosystem functioning, spatial scales, management schemes

5.2 INTRODUCTION

Interacting species of different trophic levels may respond to different components of agricultural intensification and on different spatial scales (Kruess 2003; Holland *et al.* 2004; Tscharntke *et al.* 2012). The negative effects of agricultural intensification on biodiversity and biotic interactions on local and landscape scale were focus of several studies (Tscharntke *et al.* 2005; Hendrickx *et al.* 2007; Karp *et al.* 2012) but little is known if intensification affects trophic levels differently and thereby may disrupt biotic interactions (Holt *et al.* 1999; Thies *et al.* 2003; Rand *et al.* 2012).

Moreover, different components of landscape heterogeneity, such as composition and configuration, are expected to have distinct effects on different functional groups or ecosystem processes, but this remains largely unexplored (Holzschuh *et al.* 2010; Fahrig *et al.* 2011). While composition reflects the number and proportions of different habitat types in a landscape, configuration refers to the spatial arrangement of habitats and their shapes (Li & Reynolds 1995; Fahrig *et al.* 2011). Bee abundance and species richness for instance, is enhanced by landscape composition (percentage of non-crop habitats), whereas wasps benefit from high edge density, i.e. landscape configuration (Holzschuh *et al.* 2010). Still, the role of landscape composition versus configuration for species richness and biotic interactions at different trophic levels remains unclear. Further, species may respond to landscape heterogeneity at different spatial scales depending on species-specific dispersal and foraging distances (Steffan-Dewenter 2002). For example body size (Westphal *et al.* 2006a; Greenleaf *et al.* 2007), trophic level (Thies *et al.* 2003, 2005) and resource or habitat specialisation (Tscharntke *et al.* 2005) may determine scale-dependent responses to landscape heterogeneity. Moreover, specialists of higher trophic levels are assumed to be more vulnerable to habitat fragmentation and reduced landscape heterogeneity than their hosts (Holt *et al.* 1999; Chaplin-Kramer *et al.* 2011; Brueckmann *et al.* 2011; Rand *et al.* 2012). Antagonists also have more complex requirements because they have to synchronise their activities in space and time with host abundance (Durrer & Schmid-Hempel 1995; Steffan-Dewenter 2003). Structurally diverse landscapes with great connectivity between habitats could improve the chances to find a host-occupied habitat, thereby particularly benefiting higher trophic levels.

Moreover, most studies focus on crop habitats (Tscharntke et al. 2012) while there is a lack of studies dealing with insect diversity and biotic interactions in grassland habitats, although grassland accounts for 29 % of the farmed area in Germany (http://www.bmelv-statistik.de). Local grassland management affects the structure and richness of the vegetation and thereby resource availability for arthropod communities (Borer *et al.* 2012; Socher *et al.* 2012).

Here, we used cavity-nesting bees, wasps and their antagonists in trap nests as model system to study the responses of different functional groups to local grassland management intensity and landscape heterogeneity. Trap-nesting arthropod species can serve as biodiversity indicator taxa and provide otherwise not reachable insights into multitrophic biotic interactions (Tscharntke *et al.* 1998; Steffan-Dewenter & Schiele 2008; Westphal *et al.* 2008). Hosts in this system are solitary bees, serving as pollinators of wild plants and insect-pollinated crops and predacious wasps that fulfil a crucial role as predators of pest insects (Klein *et al.* 2004). These host species depend on different habitat types within their foraging range for food supply and nest building (Westrich 1996).

Due to logistic constraints landscape-scale studies are often conducted in only one study region. However, to allow more general conclusions about impacts of different factors of landscape heterogeneity on functional biodiversity, a replication of studies in several regions is desirable (Holzschuh *et al.* 2007b; Fahrig *et al.* 2011). Here, we present results from a well replicated study conducted in 95 study plots in three distinct regions in Germany (http://www.biodiversity-exploratories.de). Within the framework of our study two questions arose. (1) What is the relative importance of local land use intensity versus landscape heterogeneity on hosts, antagonists and their interactions? (2) Are there different responses of hosts, antagonists and their interactions to landscape composition and configuration and are these responses scale-specific? To answer these questions, we tested the following hypotheses:

I. Species richness and abundance of hosts and their antagonists are negatively correlated with local land use intensity.
II. Hosts and antagonists are both enhanced by increasing landscape heterogeneity.
III. Hosts are stronger affected by landscape composition and antagonists by landscape configuration.
IV. Similar patterns across different geographic regions reveal the generality of landscape effects.

5.3 MATERIALS AND METHODS

5.3.1 Study plots

The study was conducted within the framework of the DFG-funded project 'Biodiversity Exploratories' (Fischer *et al.* 2010). The Exploratories are represented by three regions research regions in Germany (the Biosphere Reserve Schorfheide-Chorin to the National Park Hainich-Dün to the Biosphere Reserve Schwaebische Alb, henceforth referred to as Schorfheide, Hainich and Alb, http://www.biodiversity-exploratories.de). We used the experimental grassland plots of the Exploratories as study sites, where we established 3.5 x 15 m study plots (see Appendix, Table A1). The study plots were fenced with electric wire when necessary to exclude cattle. The selected grassland plots differed in their land use intensities, ranging from extensively managed calcareous grasslands to intensively used pastures and meadows with high mowing or grazing frequencies or both.

5.3.2 Trap nests

We constructed 760 trap nests using PVC tubes of 10.5 cm diameter, filled with reed internodes of *Phragmites australis* (Cav.) Trin. To sample the entire community of cavity-nesting species, we used reed of internodes with different diameters (0.2 to 1.2 cm) (Gathmann *et al.* 1994). On each study plot four wooden poles were placed in a staggered pattern with a distance of 4 m. On each pole two trap nests were mounted at 1.5 m height. Trap nests were installed between mid of April and mid of May 2008 and recollected at the end of September until beginning of October 2008. The traps were stored outside in a dry, unheated cabin to let the animals develop under natural conditions. After a diapause of a month as a cold impulse to develop, we started to dissect nests of bees and wasps in an early developmental stage to be able to record exact numbers of parasitized brood cells, cells without content due to predation and cells with dead offspring of different developmental stages (Gathmann & Tscharntke 1999; Westphal *et al.* 2008). For identification to species level, nests were closed again and then stored at room temperature until hatching of imagos.

Altogether, we quantified seven response variables: (1) the total number of brood cells, hereafter referred to as total abundance, (2) number of brood cells of hosts (bees and wasps) and (3) antagonists, (4) total species richness and (5) the number of host and (6) antagonist species, (7) parasitism rate. Mortality rate was defined as the number of dead brood cells per study site, divided by the number of total brood cells per study site. These brood cells died due to other reasons than parasitism or predation, probably due to pathogens. Parasitism rate was calculated by dividing the number of brood cells attacked by antagonists per study site by the total number of brood cells per study site.

Empty nests of multivoltine species have not been taken into account for the abundance data. For species richness data, individuals of a study site that could only be classified to higher taxonomic ranks, like genus or family rank, were only counted as additional species in case there was no other representative of the species rank on the study plot.

5.3.3 Metrics of local land use intensity

Local land use intensity was assessed by annual questionnaires and interviews with land users and land owners (Fischer *et al.* 2010). Based on this information, we calculated for each experimental plot a compound, additive index of land use intensity, hereafter termed LUI (Bluethgen *et al.* 2012). The LUI enabled the incorporation of the quantity of each component such as livestock units per hectare and duration of grazing period, number and time of mowing events and number and amount of fertilizer applications. The species number of flowering plants (FP) was calculated as the arithmetic average of two to three individual measurements (between May and September) of floral diversity on each of the 3.5 x 15 m study plots.

5.3.4 Landscape heterogeneity metrics

We mapped different land use types in the field within a radius of 2,000 m around all experimental grassland plots in 2008 and 2009. For digitalization we additionally used high resolution aerial photographs (nominal spatial resolution 0.4 m) and topographic maps (1:10,000). Using a Geographical Information System (ArcGIS^{TM} 9.3, ESRI) we classified eight general land use types: arable land, forest, grassland, semi-natural habitat, road, woodland, settlement and water bodies. Grassland comprised pastures and meadows. Semi-natural habitats comprised habitats of extensive land use, for instance extensively managed meadows, marshland, shrubland, hedges (> 5 m width), calcareous grasslands and orchards. Based on the classified raster maps of 3 x 3 m grid cells, we used the software FRAGSTATS 3.3 (McGarigal *et al.* 2002) to calculate metrics of landscape heterogeneity in the surrounding landscape of the study plots within radii of 250 m, 500 m, 750 m, 1,000 m, 1,250 m, 1,500 m, 1,750 m and 2,000 m. Landscape composition was characterised using Shannon's Diversity Index (Shannon & Weaver 1949; McGarigal *et al.* 2002). When the landscape consists of only one land use type, the Shannon's Diversity Index equals 0, reflecting that there is no diversity. With eight distinct land use types it increases to a maximum of 1.72 (2,000 m scale) in case all land use types have the same cover in the landscape. As a second metric of landscape composition, we calculated the percentage of semi-natural habitats in the landscape surrounding the study plots. It ranges from 0 % (no semi-natural habitats within the landscape) to 100 %, when the entire landscape only consists of semi-natural habitats. The Shape Index was used as metric of landscape configuration. For each dinstinct patch (continuous area of one land use type within the landscape) the ratio of patch perimeter divided by the minimum perimeter possible for a maximally compact patch (i.e. a square) of the corresponding patch area is calculated. The Shape Index is the median of those ratios and a convenient solution of the size bias of the perimeter-area ratio index by adjusting for a square standard. When the Shape Index equals one, all patches within the landscape are maximally compact while higher Shape Indices characterize more complex shapes of patches (Forman 1995).

5.3.5 Statistical analyses

We used the software R 2.14.0 for Windows (R Development Core Team 2012) for statistical analyses. To test for effects of local land use and floral richness and their interaction on the seven response variables mentioned above, we constructed ordinary linear models. For antagonist richness we additionally included host richness, for antagonist abundance we additionally included host abundance, respectively, as covariates in statistical models. Consecutively, we added landscape composition, configuration and region as explanatory variables to the models already including local variables. To test for differing effects of these variables among regions, we included interaction terms with region for each explanatory variable. We ln-transformed count data and arcsine square-root transformed percentage data when necessary to fulfil the assumption of normality of residuals (Sokal & Rohlf 1994; Crawley 2007). Species number of flowering plants was square root transformed as it generally increased the fit of models to the data. Collinearity among the explanatory variables was checked using variance inflation factors and Pearson correlation coefficients. Using thresholds of < 3 for the variance inflation factors and < 0.65 for the Pearson correlation coefficients, none of the explanatory variables were found to covary as strongly with other variables to prohibit their parallel use in models (Zuur *et al.* 2009; Zuur, Ieno & Elphick 2010). We used the dredge function of the R package MuMIn to (1) automatically construct all possible models based on the set of explanatory variables in the full model, including the null model, and to (2) identify a minimum-adequate model using the Akaike Information Criterion (AICc) for model evaluation (Burnham & Anderson 2004). First, minimum-adequate models solely based on local scale factors were identified. Second, minimum-adequate models including local and landscape factors as well as region were identified for each scale to estimate the scale on which each process and functional group responded. The spatial scale for each response variable was chosen by AICc comparison of the minimal adequate model of each scale. The model that was best supported by the data based on the lowest AICc was chosen. The improvement of model fit due to consideration of large-scale factors could then be evaluated by comparing AICc values of the best models including solely local factors with models including local, landscape factors and region. Following (Kissling & Carl 2008), spatial autocorrelation was tested calculating Moran's I values for distance classes between 1 and 10 km. In case of spatial autocorrelation we additionally calculated spatial linear models. The spatial linear models were calculated as 'spatial simultaneous autoregressive error models' using the R library 'spdep', v. 0.5-41 (Bivand 2012). Generally, Moran's I correlograms revealed spatial autocorrelation in the minimal adequate models for total species richness and species richness of hosts as well as their corresponding abundances and mortality rate (Table 9). However, they yielded similar estimates like the corrected SARerr models so that it was justified to rely on Ordinary-Least-Squares-Models without correction (Table 8).

5.4 RESULTS

A total of 3,672 nests with 19,603 brood cells were collected yielding 12,786 individuals, of which 8,070 were males and 4,716 females. Most of the brood cells were occupied by host species (18,082). Antagonists were found in 1,390 of the brood cells and 103 cells harboured generalist predators. Altogether, 75 species could be identified, from which 48 were host species and 27 antagonists. Half of the host species were wasps and the other half were bees (24 species each). The 27 species of antagonists consisted of three bee species, two predatory beetles, two parasitoid flies and 20 species of parasitoid wasps (Table A6). The total number of species and composition of communities varied between regions. The Alb comprised 51, Hainich 35 and Schorfheide 43 species. The community composition in Alb and Schorfheide differed in 52 species, Alb and Hainich in 27 and Hainich and Schorfheide in 28 species (Table A6).

5.4.1 Regional differences in hymenoptera communities and land use intensity

Total species richness varied significantly between regions ($F_{2,92} = 5.054$, $P = 0.008$). This was due to significant differences in host species richness ($F_{2,92} = 8.779$, $P < 0.001$), whereas antagonist species richness did not vary significantly between regions ($F_{2,92} = 0.879$, $P = 0.419$) (Fig. 13a). Total abundance, measured as number of brood cells per study site, as well as abundance of hosts and antagonists did not vary significantly between regions (Fig. 13b). Parasitism rate ($F_{2,92} = 3.74$, $P = 0.027$) varied significantly between regions (Fig. 13c).

The range of the LUI was similar in all three regions, though the median was highest in the Alb and lowest in the Schorfheide (Table 6). The most important scales, each functional group responded to, were 250 and 1,500 m. Landscape metrics for these scales revealed no big differences between the different regions (Table 6, Table A7). The Shape Index (1,500 m) was similar in Alb and Hainich, and covered a slightly wider range in the Alb. In the Schorfheide, the median and range of the Shape Index (1,500 m) was lower while simultaneously the median and range of the Shannon's Diversity Index was higher. The percentage of semi-natural habitats on a scale of 250 m had the lowest range in the Schorfheide, while Hainich and Alb had similar ranges. On a scale of 1,500 m, the range of the percentage of semi-natural habitats in the Alb also overtopped the range in Hainich, while the medians remained similar (Table 6).

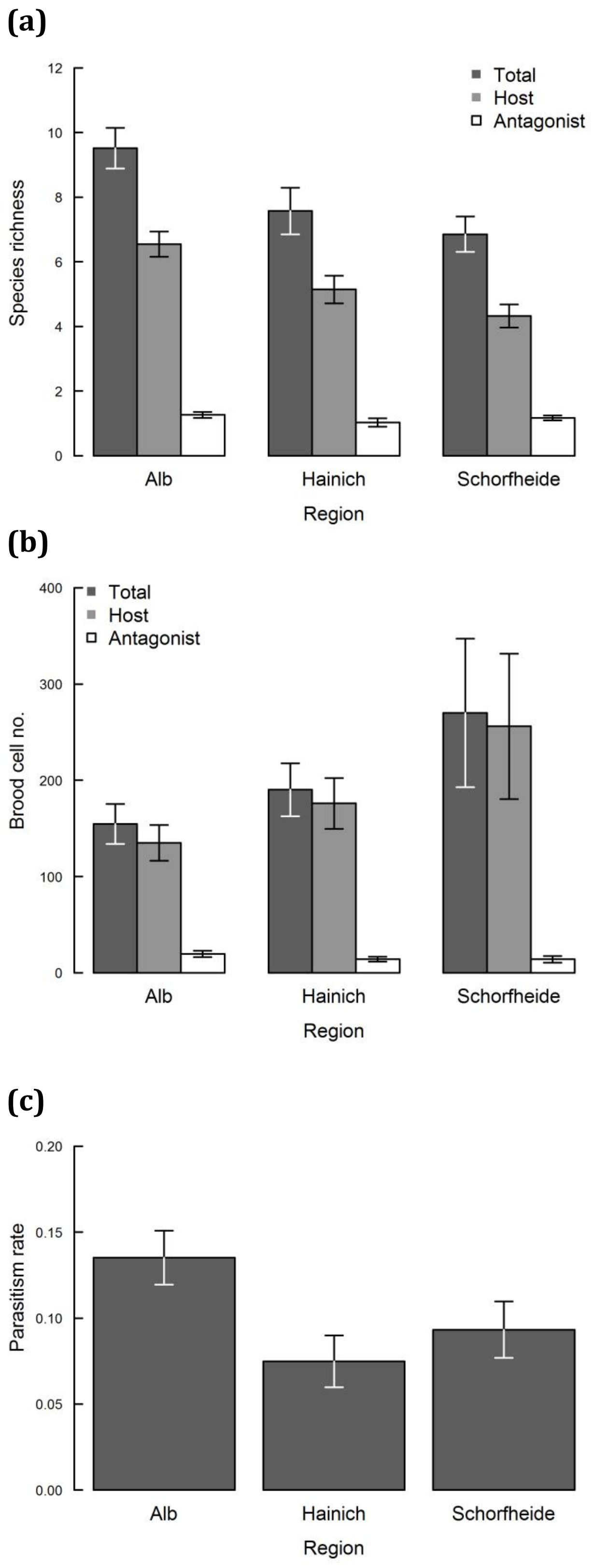

Figure 13 (a) Effects of region on means (±SE) of species richness of all trap-nesting species, host species and antagonist species on plot level.

(b) Effects of region on means (±SE) of brood cell numbers of all trap-nesting individuals, hosts and antagonists on plot level.

(c) Effects of region on means (±SE) of parasitism rate of all trap-nesting individuals, hosts and antagonists on plot level. Letters over bars show significant differences at $P < 0.05$ by pairwise t-tests with Bonferroni correction ($\alpha = 0.0167$).

Table 6 Median, minimum and maximum values of local and landscape scale factors for 95 grassland plots of 250 m and 1,500 m radius in each region in 2008/2009. LUI = Land use index, FP = Species number of flowering plants, SHAPE = Median of the Shape index, SHDI = Shannon's diversity index, % SNH = Percentage of semi-natural habitats

Region	**Local level**				**Landscape level 250 m**						**Landscape level 1500 m**					
	LUI	**min-max**	**FP**	**min-max**	**SHAPE MD**	**min-max**	**SHDI**	**min-max**	**% SNH**	**min-max**	**SHAPE MD**	**min-max**	**SHDI**	**min-max**	**% SNH**	**min-max**
Alb	0.2318	0.01-0.59	28.0	8-97	1.6250	1.33-2.11	0.9379	0.39-1.37	4.8345	0.00-86.85	1.7632	1.47-2.37	1.3547	0.84-1.64	6.4083	0.52-61.45
Hainich	0.1551	0.01-0.54	28.5	0-72	1.5633	1.13-1.93	1.0637	0.00-1.42	5.4639	0.00-83.21	1.7540	1.31-2.14	1.4208	0.79-1.59	7.8415	1.07-41.81
Schorfheide	0.1121	0.03-0.59	17.0	0-52	1.5127	1.16-2.03	0.7430	0.24-1.30	4.2655	0.00-21.02	1.6581	1.41-1.91	1.4276	1.01-1.72	7.6189	0.83-13.77

5.4.2 Local and landscape scale effects

Minimum-adequate models including landscape factors and region as explanatory variables were generally better supported in terms of AICc values than models incorporating only local scale variables (Table 7), underscoring the importance of landscape and regional scale factors in determining diversity, abundance and the strength of host-antagonist-interactions in grassland animal communities.

Table 7 Model comparison of minimal adequate models based on solely local scale effects vs. models including large scale effects as well.

Response variable		Scale of explanatory variables	
		Local	Local, landscape and regional
Species richness			
Total species richness	df	3	5
	AICc	511.82	494.49
Species richness of hosts	df	3	6
	AICc	420.15	405.15
Species richness of antagonists	df	5	6
	AICc	127.65	124.48
Abundance			
Total number of brood cells	df	3	8
	AICc	292.01	271.06
Brood cell number of hosts	df	3	8
	AICc	295.32	274.74
Brood cell number of antagonists	df	3	5
	AICc	317.41	278.02
Parasitism rate	df	2	5
	AICc	119.34 ♦	101.01

♦ Null model is given.

For each response variable the selected minimum-adequate model is given in Table 8 and 9. In the following, we present the effect directions and strengths of variables of the minimum-adequate models. The most predictive scale for total species richness as well as species richness of hosts was at 250 m (Table 8, Table 9).

Table 8 Model estimates of minimal adequate models for each response variable on the corresponding scale. Explanatory variables incorporated in each model are listed for each response variable individually. Model factors for the OLS and the SARerr model are listed side by side for a better comparison. Abundances were ln-transformed as well as parasitism rate and species richness of antagonists, % semi-natural habitats was arcsine-square-root-transformed. FP was square-root-transformed. SHDI = Shannon's diversity index, SHAPE = Median of the Shape index. Signif. codes: P < 0.001: ***, P < 0.01: **, P < 0.05: *

			OLS model			SARerr model		
Response variable	**Scale [m]**	**Explanatory variable**	**Estimate**	**t**	**p**	**Estimate**	**z**	**p**
Species richness								
Total species richness	250	Intercept	1.9295	1.454	0.1494	1.0517	1.045	0.2958
		SHDI index	4.0905	3.899	0.0002 ***	4.1531	4.267	< 0.0001 ***
		% seminat. habitats	2.7971	1.991	0.0495 *	2.2956	1.695	0.0901
		Number of plant species	0.7884	0.512	0.1273	1.2465	2.828	0.0047 **
Species richness of hosts	250	Alb	3.5982	4.974	< 0.0001 ***	3.7415	5.048	< 0.0001 ***
		Hainich	2.5027	-2.152	0.0341 *	2.6447	-1.818	0.0691
		Schorfheide	2.2110	-2.734	0.0075 **	2.3516	-2.346	0.0190 *
		SHDI index	2.1915	3.294	0.0014 **	2.0177	3.126	0.0018 **
		% seminat. habitats	2.3448	3.100	0.0026 **	2.3633	3.254	0.0011 **
Species richness of antagonists	1500	Alb	-1.0246	-1.625	0.1077	-1.0011	-1.625	0.1041
		Hainich	-1.0465	-0.185	0.8537	-1.0261	-0.251	0.8021
		Schorfheide	-0.7092	2.558	0.0122 *	-0.6900	2.922	0.0035 **
		SHAPE index	0.7226	2.094	0.0391 *	0.7203	2.138	0.0325 *
		Spec. richn. of hosts	0.1532	7.195	< 0.0001 ***	0.1502	7.253	< 0.0001 ***
Abundance								
Total number of brood cells	250	Alb	5.0010	7.509	< 0.0001 ***	5.0584	7.594	< 0.0001 ***
		Hainich	3.3451	-2.022	0.0462 *	3.4046	-2.024	0.0430 *
		Schorfheide	3.1174	-2.444	0.0165 *	3.7156	-1.678	0.0934
		Alb:SHDI index	0.0444	0.068	0.9463	-0.1329	-0.212	0.8319
		Hainich:SHDI index	1.9217	2.233	0.0281 *	1.8862	2.637	0.0084 **
		Schorfheide:SHDI index	2.4271	2.823	0.0059 **	1.6301	2.153	0.0313 *
		LUI index	-1.2056	-1.954	0.0538	-0.9418	-1.639	0.1011
Brood cell number of hosts	250	Alb	4.9713	7.322	< 0.0001 ***	4.9993	7.359	< 0.0001 ***
		Hainich	3.2813	-2.024	0.0460 *	3.3410	-1.988	0.0468 *
		Schorfheide	2.9533	-2.568	0.0119 *	3.5891	-1.726	0.0843
		Alb:SHDI index	-0.0831	-0.124	0.9015	-0.2323	-0.364	0.7155
		Hainich:SHDI index	1.8900	2.302	0.0237 *	1.8471	2.669	0.0076 **
		Schorfheide:SHDI index	2.5024	3.005	0.0035 **	1.6528	2.261	0.0238 *
		LUI index	-1.1747	-1.868	0.0651	-0.8847	-1.513	0.1302
Brood cell number of antagonists	1500	Intercept	-5.5402	-3.998	0.0001 ***	-5.7575	-4.098	< 0.0001 ***
		SHAPE index	2.5216	3.427	0.0009 ***	2.5480	3.479	0.0005 ***
		Number of plant species	0.2781	2.027	0.0456 *	0.2862	2.038	0.0416 *
		Brood cell no.of hosts	0.5855	6.344	< 0.0001 ***	0.6141	6.876	< 0.0001 ***
Parasitism rate	1500	Alb	-3.7989	-6.916	< 0.0001 ***	-3.8510	-7.521	< 0.0001 ***
		Hainich	-4.1101	-3.044	0.0031 **	-4.1624	-4.821	< 0.0001 ***
		Schorfheide	-3.8990	-0.986	0.3265	-3.9437	-1.373	0.1697
		SHAPE index	1.2794	4.169	< 0.0001 ***	1.3093	4.562	< 0.0001 ***

Table 9 Overview over minimal adequate models for each response variable. Multiple R^2 and AICc values are given for Ordinary-Least-Squares-Models (OLS) as well as Spatial-Error-Models (SARerr) for comparison. Moran's I values refer to the smallest spatial scale of 1 km and indicate the degree of spatial autocorrelation of residuals derived from the OLS model. First local explanatory variables are given (LUI = Land use index, FP = Species number of flowering plants, SR host = Species richness of hosts, BC host = Brood cell number of hosts), then the identified adequate scale for the following landscape factors (SHDI = Shannon's diversity index, SHAPE = Median of the Shape index, % SNH = Percentage of semi-natural habitats). Arrows indicate that a variable was part of the minimal adequate model and give the effect direction. Significant interactions between region and any other explanatory variable are shown by differing colours between regions. (yellow: Alb, red: Hainich, blue: Schorfheide). Thinner arrows indicate non-significant effects (P > 0.05). The incorporation of region in the minimum adequate model is indicated by a circle.

	OLS Model			**SARerr Model**		**Explanatory variable**								
Response variable	**R^2**	**AICc**	**Moran's I**	**R^2**	**AICc**	**Local scale variables**				**Scale [m]**	**Large scale variables**			**Region**
Species richness						LUI	FP	SR host	BC host		SHDI	SHAPE	% SNH	
Total species richness	0.2862	494.49	0.368	0.3055	494.17		↗			250	↗		↗	
Species richness of hosts	0.3426	405.15	0.284	0.3470	406.84					250	↗		↗	●
Species richness of antagonists	0.4036	124.48	0.136	0.4047	126.62			↗		1500		↗		●
Abundance														
Total number of brood cells	0.3090	271.06	0.314	0.3479	268.01	↘				250	↗↗↗			●
Brood cell number of hosts	0.3053	274.74	0.347	0.3459	271.46	↘				250	↘↗↗			●
Brood cell number of antagonists	0.3862	278.02	0.091	0.3985	278.38		↗		↗	1500		↗		●
Parasitism rate	0.2303	101.01	-0.016	0.2515	100.65					1500		↗		●

Shannon's Diversity Index as well as the percentage of semi-natural habitats were positively correlated with total species richness as well as species richness of hosts on the scale of 250 m. Contrary to the best model for host species richness, the best model for total species richness did not include region but species number of flowering plants. However, effects of Shannon's Diversity Index and the percentage of semi-natural habitats on species richness of hosts were consistent among regions (N = 95, P < 0.01; Table 8, Fig. 14a). Total abundance was enhanced by Shannon's Diversity Index (250 m) in all three regions. Differing effects on host abundance between regions were not significant (Table 8). Based on the AICc model selection, both best models also included local land use intensity which negatively affected abundance. In the Alb no effect of Shannon's Diversity Index on host abundance was detected (N = 33, P > 0.1) whereas in the Hainich (N = 28, P < 0.01) and in the Schorfheide (N = 34, P < 0.001) host abundance significantly increased with Shannon's Diversity Index (Fig. 14b).

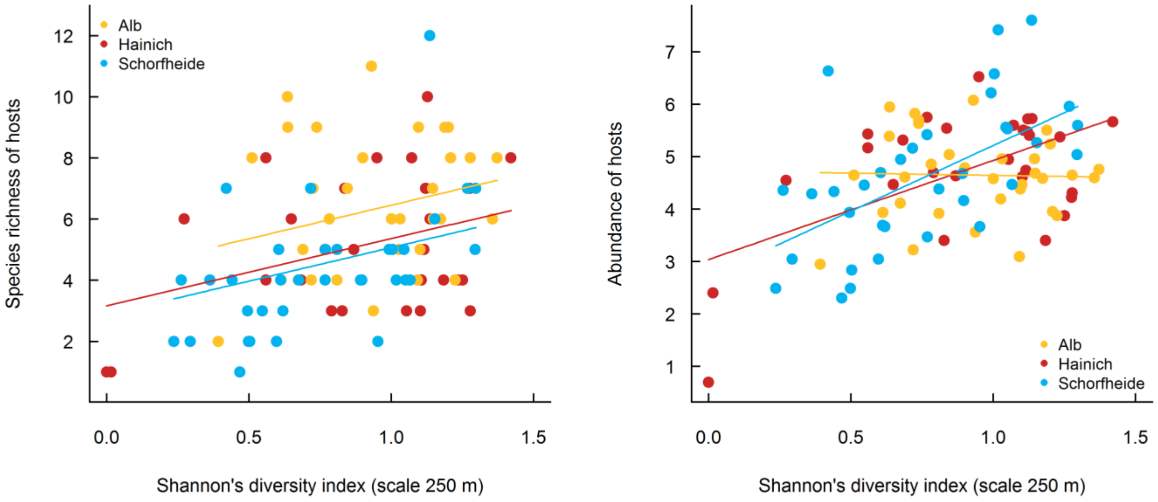

Figure 14 (a) Species richness of hosts was positively correlated with Shannon's diversity index (SHDI). (b) Abundance of hosts (ln-transformed) responded to a significant interaction between SHDI and region. If there were further variables in the model, they were set up to mean

In contrast, species richness and abundance of antagonists were significantly positively correlated with the Shape Index on a scale of 1,500 m (Fig. 15a, 15b; Table 3, Table 4), but neither with local land use intensity, nor Shannon's Diversity Index, nor the percentage of semi-natural habitats. Species richness of flowering plants positively affected the abundance of antagonists (Table 8, Table 9). The abundance

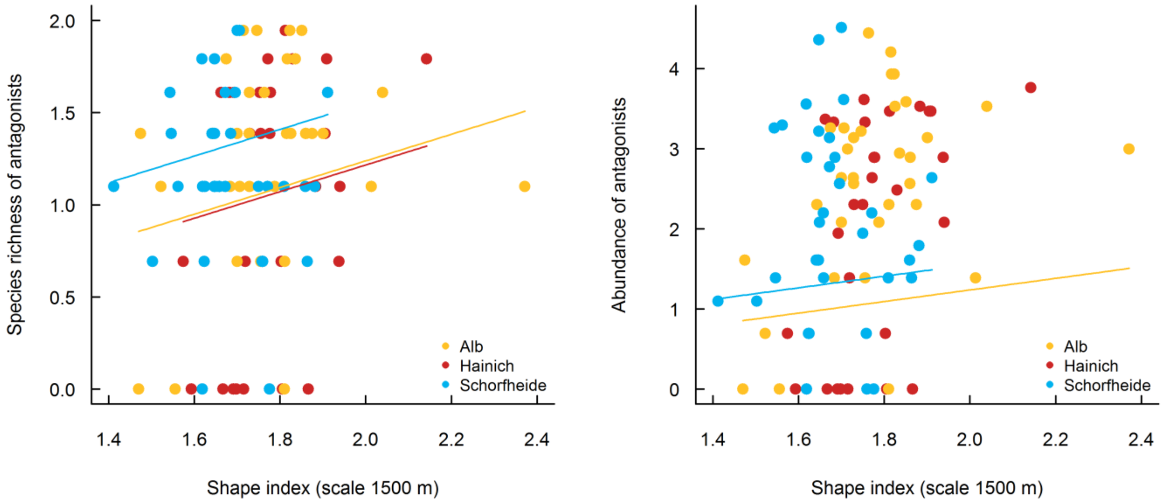

Figure 15 (a) Species richness of antagonists (ln-transformed) plotted against the Shape index for each region. (b) Abundance of antagonists (ln-transformed) was positively affected by the Shape index in each region. If there were further variables in the model, they were set up to mean values.

of hosts also had a significant positive impact on the abundance of antagonists (Table 8). Likewise species richness of antagonists responded significantly positively to species richness of hosts (Table 8). Moreover, local diversity of antagonists was positively correlated with parasitism rate (lm: $F_{1,93} = 30.86$, $P < 0.001$). Parasitism rate was significantly positively correlated with the Shape Index on a scale of 1,500 m in all three regions (Fig. 16, Table 8, Table 9).

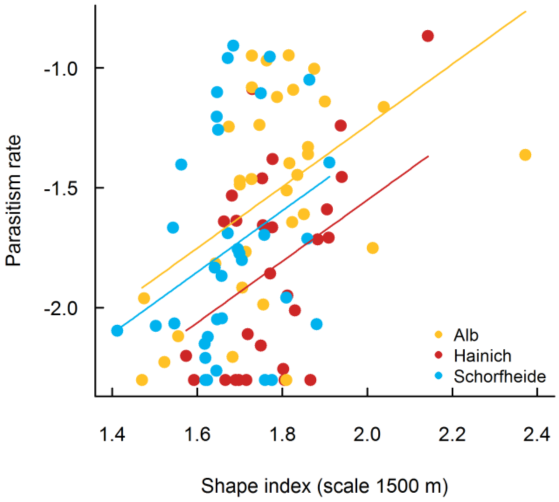

Figure 16 Parasitism rate (ln-transformed) was positively correlated with the Shape index in each region. If there were further variables in the model, they were set up to mean values.

5.5 DISCUSSION

In this study we aimed to disentangle effects of land use intensification across spatial scales on interacting species groups of solitary bees and wasps and their antagonists to be able to draw up conservation schemes that counteract these effects specifically. Landscape scales were more relevant than local scales in explaining patterns of species richness, abundance and biotic interactions. Importantly, we found that host species responded to a diversely composed landscape at small spatial scales whereas their antagonists benefitted from a spatially complex landscape at large spatial scales.

As hypothesised, total species richness and abundance were enhanced by landscape heterogeneity, in particular by Shannon's Diversity Index and the percentage of semi-natural habitats whereas local management intensity of grasslands played a minor role. Semi-natural areas surrounding agricultural habitats are considered to serve as source for (re)colonisation of managed areas (Tscharntke *et al.* 2012). Thus, bees and wasps were rather promoted on landscape than on local scales (Swift, Izac & van Noordwijk 2004; Tscharntke *et al.* 2005). Likewise, for other insect taxa landscape structure was found to be more important than farming system (Weibull, Bengtsson & Nohlgren 2000; Fahrig *et al.* 2011; Tscharntke *et al.* 2012).

The analysis of multiple spatial scales was useful to account for different dispersal and foraging distances of species groups that might respond to landscape parameters on different spatial scales. In contrast to expectations, the antagonists responded to larger spatial scales (1,500 m) than their lower trophic level hosts (250 m) (Holt 1996). Other patterns were found in a former trap nest study where the abundance of antagonists was positively affected by the percentage of semi-natural habitats on a smaller scale (500 m) than host species richness (up to 750 m) (Steffan-Dewenter 2002). Also a thistle-study revealed larger home ranges for herbivores (> 3,000 m) than for their parasitoids (750 m) (Kruess 2003). Contradictory responses of interacting species on spatial scales might be explained by different degrees of specialisation or regional differences on higher trophic level interactions (Kruess & Tscharntke 1994; Rand *et al.* 2012). Further, the dependency on host populations that fluctuate in time and space, might result in higher dispersal rates of antagonists (Thies *et al.* 2003) to compensate for local resource limitation.

Local resource limitation alone does not seem to harm host species and their antagonists as long as landscape structure provides additional food resources for bees and wasps and supports dispersal of their antagonists. Nevertheless, grasslands might provide more local resources than crop habitats thereby explaining contradicting results in a trap nest community study in wheat fields (Holzschuh *et al.* 2010). The differing responses of hosts and antagonists may have consequences for pollination services and population control: pollinating bees may offer their service within several hundred meters (Ricketts *et al.* 2008) if a landscape provides a diversity of habitats while their antagonists can only control populations if habitat connecting corridors over large spatial scales are given.

We could verify our hypothesis, that hosts were positively affected by a high Shannon's Diversity Index and a high percentage of semi-natural habitats (landscape composition). If a variety of different habitats, like hedges with potential nesting opportunities and flower-rich meadows, were reachable for these central-place-foragers, they occurred in high abundances and species numbers. Hosts as species of lower trophic level only required the mentioned habitat mix or a highly diverse patch of semi-natural habitat. Therefore, their occurrence and thus species richness was mediated by landscape metrics. In contrast to our hypothesis, host abundance only marginally depended on local conditions (LUI). Females of bees and wasps will prefer to nest where local conditions favour their food and nesting resources. We assume that local species occurrence despite unfavourable local conditions was facilitated by small-scaled landscape heterogeneity and provision of additional food resources.

Our results indicate that antagonists profit more from landscape configuration than landscape composition. Species richness and abundance of antagonists, as well as parasitism rate, were enhanced by the Shape Index (landscape configuration) at a large spatial scale (1,500 m). These findings are in accordance with studies on local prey/host losses that revealed that antagonists depend more than their hosts on connected habitats to switch between them (Tscharntke & Kruess 1999). Antagonists require habitats with phenologically matching occurrence of (certain) hosts. Presumably, the probability to find suitable habitats is higher in a landscape with sufficient non-arable habitats and edge structures that connect potential host habitats. Connective elements and edge structures should not only maintain dispersal of antagonists but also supply natural nesting resources in hedges or forest edges for potential hosts. Antagonists attracted by these conditions consequently occur in higher abundances if the Shape Index is high. These naturally abundant antagonists may be the reason for higher parasitism rates in local trap nests.

The abundance of antagonists was enhanced by species number of local flowering plants, contrary to a recent study of (Ebeling *et al.* 2012). An enhanced floral richness might also imply a structural richness of the vegetation, offering food supply and shelter for predators and parasitoids and for antagonists that directly depend on flowers for feeding on nectar (Westrich 1989).

The general relation of biodiversity and ecosystem functioning is still controversially discussed. Depending on four mechanisms (redundancy, idiosyncrasy, species complementarity and sampling effects) there might be a correlation of species richness and ecosystem functioning or not (Tscharntke *et al.* 2005). Our study indicates that local species richness of antagonists is positively correlated with ecosystem functions like population control through parasitism. This is in accordance with former trap-nest studies (Tscharntke *et al.* 1998; Veddeler *et al.* 2010).

It might depend on the region studied whether a landscape metric affects species richness or not (Gimona, Messager & Occhi 2009; Fahrig *et al.* 2011). The mean species richness per region declined from south to north. This might be explained by differing biotic (below- and aboveground species pool) and abiotic (climate) or socio-economic (agricultural practices) conditions across regions (Gaston 2000; Fahrig *et al.* 2011; Tscharntke *et al.* 2012). Nevertheless, for most dependent variables we could find consistent, general patterns independently of region, because there were no significant interactions with region in the final models. This indicates that our results regarding landscape composition and configuration are of general significance across different regions. Future studies could benefit from an even higher number of replicates at the region level and the selection of regions with more contrasting landscape characteristics.

To conclude, we could show with a highly replicated large-scale field study that hosts and their antagonists respond to different components of landscape heterogeneity at different spatial scales. To facilitate host species (pollinators and predators), small-scale measures that involve a diversification of the surrounding matrix are needed. The requirements of their antagonists could be better promoted by management schemes that address landscape configuration, e.g. by creating edge habitats and connecting corridors at larger spatial scales. Hence, to facilitate trophic interactions and valuable ecosystem services offered by different functional groups, management measures should specifically address landscape diversity and spatial complexity by reducing the size of grasslands and creating a multitude of different, complex shaped habitats with unmanaged field margins within a radius of 1.5 km.

5.6 APPENDIX

Table A6 (part 1) Species composition of trap nest species for each region sorted by function

Species	Alb	Hainich	Schorfheide	Function
Chelostoma florisomne (Linnaeus)	x	x	x	host bee
Hylaeus communis (Nylander)	x	x	x	host bee
Megachile alpicola (Alfken)	x	x	x	host bee
Megachile versicolor (Smith)	x	x	x	host bee
Osmia leaiana (Kirby)	x	x	x	host bee
Osmia leucomelana (Kirby)	x	x	x	host bee
Osmia parietina (Curtis)	x	x	x	host bee
Osmia rufa (Linnaeus)	x	x	x	host bee
Heriades truncorum (Linnaeus)	x	x		host bee
Anthophora furcata (Panzer)	x			host bee
Chelostoma distinctum (Stoeckhert)	x			host bee
Hylaeus confusus (Nylander)	x			host bee
Osmia claviventris (Thomson)	x			host bee
Osmia gallarum (Spinola)	x			host bee
Chelostoma rapunculi (Lepeletier)		x		host bee
Hylaeus angustatus (Schenck)		x		host bee
Megachile ericetorum (Lepeletier)		x		host bee
Megachile centuncularis (Linnaeus)		x	x	host bee
Hylaeus difformis (Eversmann)			x	host bee
Osmia caerulescens (Linnaeus)			x	host bee
Osmia cerinthidis (Morawitz)			x	host bee
Osmia mustelina (Gerstaecker)			x	host bee
Osmia niveata (Fabricius)			x	host bee
Ancistrocerus gazella (Panzer)	x	x	x	host wasp
Ancistrocerus trifasciatus (Müller)	x	x	x	host wasp
Euodynerus quadrifasciatus (Fabricius)	x	x	x	host wasp
Symmorphus gracilis (Brullé)	x	x	x	host wasp
Trypoxylon figulus (Linnaeus)	x	x	x	host wasp
Ancistrocerus nigricornis (Curtis)		x	x	host wasp
Ancistrocerus parietinus (Linnaeus)		x	x	host wasp
Gymnomerus laevipes (Shuckard)	x	x		host wasp
Passaloecus borealis (Dahlbom)	x	x		host wasp
Passaloecus corniger (Shuckard)	x	x		host wasp
Passaloecus gracilis (Curtis)	x	x		host wasp
Ancistrocerus claripennis (Thomson)	x			host wasp
Crossocerus barbipes (Dahlbom)	x			host wasp
Passaloecus eremita (Kohl)	x			host wasp
Passaloecus insignis (Vander Linden)	x			host wasp
Pemphredon lugens (Dahlbom)	x			host wasp
Pemphredon morio (Vander Linden)	x			host wasp
Symmorphus allobrogus (Saussure)	x			host wasp
Dipogon bifasciatus (Geoffroy)	x		x	host wasp
Ancistrocerus antilope (Panzer)			x	host wasp
Discoelius dufourii (Lepeletier)			x	host wasp
Pemphredon rugifera (Dahlbom)			x	host wasp
Symmorphus angustatus (Zetterstedt)			x	host wasp
Symmorphus murarius (Linnaeus)			x	host wasp

Table A6 (part 2)

Species	Alb	Hainich	Schorfheide	Function
Coelioxys inermis (Kirby)		x	x	parasitoid bee
Stelis phaeoptera (Kirby)		x	x	parasitoid bee
Coelioxys mandibularis (Nylander)		x		parasitoid bee
Cacoxenus indagator (Loew)	x	x	x	parasitoid fly
Anthrax anthrax (Schrank)	x		x	parasitoid fly
Chrysis ignita B-Gruppe	x	x	x	parasitoid wasp
Chrysis solida (Haupt)	x	x	x	parasitoid wasp
Ephialtes manifestator (Linnaeus)	x	x	x	parasitoid wasp
Melittobia acasta (Walker)	x	x	x	parasitoid wasp
Trichrysis cyanea (Linnaeus)		x	x	parasitoid wasp
Monosapyga clavicornis (Linnaeus)		x		parasitoid wasp
Chrysura radians (Harris)	x			parasitoid wasp
Dusona juvenilis (Forster)	x			parasitoid wasp
Ephialtes zirnitsi (Ozols)	x			parasitoid wasp
Gasteruption assectator (Linnaeus)	x			parasitoid wasp
Omalus aeneus (Fabricius)	x			parasitoid wasp
Perithous scurra (Panzer)	x			parasitoid wasp
Poemenia collaris (Haupt)	x			parasitoid wasp
Poemenia notata (Holmgren)	x			parasitoid wasp
Pseudomalus auratus (Linnaeus)	x			parasitoid wasp
Gasteruption jaculator (Linnaeus)	x		x	parasitoid wasp
Sapyga quinquepunctata (Fabricius)	x		x	parasitoid wasp
Chrysis graelsii (Guérin)			x	parasitoid wasp
Chrysis iris (Christ)			x	parasitoid wasp
Chrysis pseudobrevitarsis (Linsenmaier)			x	parasitoid wasp
Megatoma undata (Linnaeus)	x	x	x	predator
Trichodes apiarius (Linnaeus)	x		x	predator
Alpha-Diversity	**51**	**35**	**43**	
Beta-Diversity	**Alb:Hainich=27**	**Hainich:Schorfheide=28**	**Alb:Schorfheide=52**	

Table A7 Median, minimum and maximum values of landscape factors for a selection of 95 grassland plots within a radius of 250 m in 2008/2009. % SNH = percentage of semi-natural habitats

	% Arable land		% Grassland		% Forest		% SNH		% Road		% Woodland		% Urban area		% Water	
Region	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**	**Median**	**Min-max**
Alb	1.92	0-31.19	38.64	0-89.97	22.31	0-70.87	4.83	0-86.85	0.00	0-2.08	1.01	0-14.59	0.00	0-12.50	0.00	0-0.51
Hainich	11.57	0-57.03	50.66	0-100	12.32	0-64.74	5.46	0-83.21	0.00	0-2.15	0.64	0-24.26	0.00	0-6.35	0.00	0-0
Schorfheide	0.26	0-49.94	77.23	22.33-94.91	1.00	0-55.38	4.27	0-21.02	0.00	0.2.32	0.98	0-12.64	0.00	0-24.62	0.00	0-19.15

6 CHAPTER IV

Spatially complex landscapes enhance the foraging efficiency of a solitary bee (*Osmia bicornis*)

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(in preparation)

6.1 ABSTRACT

Land use intensification affects the amount and spatial distribution of resources at local and landscape scales, but consequences for the reproduction of solitary bees that rely on pollen and nectar resources within their foraging range are little explored. We analysed the relative importance of local land use intensity and landscape composition and configuration for pollen-nectar trips. Further, we hypothesize a benefit of short pollen-nectar trips for the reproductive success of local bee populations.

To test this hypothesis, we released 50 female Red Mason Bees (*Osmia bicornis*) at each of 18 study sites in two geographic regions in Germany and provided reed stem bundles as nesting resources. We observed time budgets for pollen foraging trips and other nest building activities and subsequently measured the reproductive success.

We found a decrease in median foraging trip duration in spatially complex landscapes. Neither local flower cover, nor land use intensity, nor landscape composition could explain foraging patterns. In contrast to our expectations, we found no evidence for a positive influence of shorter foraging trips on the reproductive success of the Red Mason Bee.

Our results suggest that solitary bees benefit from spatially complex landscapes that provide a higher density and temporal stability of floral resources. Thus agri-environment schemes should aim to structure landscapes by means of hedges, sown field margins or other linear elements to maintain abundant and diverse pollinator communities.

Key-Words: foraging trip durations, trap nests, *Osmia bicornis*, *Osmia rufa*, land use intensity, flower cover, landscape composition, reproductive success, parasitism rate, sex ratio

6.2 INTRODUCTION

Land use intensification in the past led to a reduction of plant diversity and pollinator diversity at local and landscape scales (Holzschuh *et al.* 2007a; Socher *et al.* 2012). Bees as important pollinators and central place foragers are especially sensitive to these land use changes, as they depend on floral and nesting resources within a limited home range (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007). Bee species diversity is declining as well as plants that rely on insect pollination (Biesmeijer et al. 2006). Local diversity of flowering plants, landscape heterogeneity and mass-flowering crops are known to positively affect richness and abundance of solitary bees (Tylianakis *et al.* 2006; Williams & Kremen 2007; Jauker *et al.* 2012; Holzschuh *et al.* 2012). However, the underlying mechanisms, spatial scales and components of landscape heterogeneity that drive the decline of pollinator populations remain poorly studied (Fahrig *et al.* 2011; Jha & Kremen 2013).

One rarely studied mechanism how land use intensification may translate into the decline of bee populations is the efficiency of foraging by bees (Gathmann & Tscharntke 2002). *Osmia bicornis*, for instance, needs 80 % of the total time of nest construction to forage for food (Maddocks & Paulus 1987; Strohm *et al.* 2002). The more time and energy a bee has to spend to forage for pollen and nectar, the less offspring can be produced (Peterson & Roitberg 2006b; Zurbuchen *et al.* 2010a). A resource-rich environment could lead to a reduction of foraging trip duration and thereby enhance reproductive success (Westphal *et al.* 2006b). Foraging efficiency and thus the number of offspring and sex allocation decisions are known to depend on resource availability (Peterson & Roitberg 2006a; Westphal, Steffan-Dewenter & Tscharntke 2009) and individual body size (Seidelmann, Ulbrich & Mielenz 2010). Moreover, higher temperatures are known to enhance the foraging efficiency of *O. bicornis* (Strohm *et al.* 2002). Population modelling suggests that decreasing habitat quality could shift the sex ratio of a solitary bee to more males, as they need less provision than the daughters (Ulbrich & Seidelmann 2001), but empirical data are lacking so far.

For mobile organisms such as solitary bees, both local and landscape characteristics are important to fulfil requirements for reproduction (Williams & Kremen 2007; Holzschuh *et al.* 2012). The Red Mason Bee *Osmia bicornis* (Synonym *O. rufa*) is a polylectic generalist that builds linear nests with up to 20-30 brood cells in pre-existing cavities in dead wood, shrubs, herbs or trap nests. Loam is used to partition brood cells and seal the nest entrance (Westrich 1996). During its nest building activities from March to June, *O. bicornis* relies on constant pollen and nectar supply in the vicinity of the nest. Estimated foraging ranges are about 600-800 m (Gathmann & Tscharntke 2002). Brood cells of *O. bicornis* are attacked by several natural antagonists (Steffan-Dewenter & Schiele 2008).

Natural enemies can potentially control natural host populations. However for *O. bicornis*, inverse density-dependent parasitism indicated that population growth was rather limited by habitat factors like food and nesting resources than regulated by top-down forces like natural enemies (Steffan-Dewenter & Schiele 2008). Yet, the risk of open cell parasitism was found to increase with provisioning time per cell (Seidelmann 2006). Moreover, more enemy species occurred with increasing proportion of semi-natural habitats (Steffan-Dewenter 2002).

To our knowledge, no study considered so far the importance of compositional versus configurational landscape heterogeneity for provisioning of food and nest building resources for solitary bees and potential adverse effects of natural enemies. In this study, we tested the effects of local land use intensity, landscape configuration and composition on the foraging efficiency (i.e. the duration of foraging trips) of *O. bicornis*. We also analysed time budgets for other components of nest building activities. We hypothesise that longer pollen-nectar trips (henceforth referred to as foraging trips/times) are compensated by reducing the time spent for other activities like partition building. Further, we asked whether the duration of foraging trips affects different components of reproductive success, namely (1) the number of brood cells, (2) total offspring biomass, (3) the sex ratio, (4) mortality rate, and (5) parasitism rate.

6.3 MATERIALS AND METHODS

The study was conducted on 18 grassland sites (see Appendix, Table A8) in two geographic regions in Germany, ten sites in the 'Biosphere Reserve Schwäbische Alb' and eight in the 'National Park Hainich-Dün' (henceforth referred to as Alb and

Hainich) within the framework of the Biodiversity Exploratories (see (Fischer *et al.* 2010) for details on study regions.

6.3.1 Experimental setup

At each site, a 3.5 m x 15 m plot was established and in case of cattle presence fenced with electric wire. To provide sufficient nesting sites and to record the reproductive success of *O. bicornis*, we installed eight trap nests on each plot. A total of 144 trap nests were constructed by filling PVC tubes of 10.5 cm diameter with internodes of reed *(Phragmites australis)*(Krombein 1967; Gathmann *et al.* 1994). The trap nests were mounted on two wooden posts at a height of 1.5 m. Additional to the LUI, we assessed the cover of potential food plants of *O. bicornis* in cm^2 within the 3 x 15 m study plot for each observation survey and calculated the mean flower cover per plot for the entire season. It ranged between study plots from 79 cm^2 to 10,267 cm^2 (mean ± SE, 2099.16 ± 721.99).

In May, we exposed eight reed stem trap nests and a box with 50 hibernated female cocoons of *O. bicornis* on each study site and simultaneously released approximately 30 adult males (mean ± SE, 31.94 ± 2.58) for copulation. We expected the emerged females to colonize the nearby trap nests. After collection from the field in September, the nests containing cocoons of the offspring were stored in a climate chamber at 4°C to give an earlier cold impulse to develop. Subsequent dissection of the nests started in October.

6.3.2 Local and landscape metrics

We mapped eight land use types (arable land, forest, grassland, semi-natural habitats, road, woodland, settlement, water bodies) within 2,000 m of the surrounding landscape of each study site using a Geographical Information System (ArcGIS™ 9.3, ESRI). Semi-natural habitats included extensively managed meadows, marshland, shrubland, hedges, calcareous grasslands and orchards. The mapping campaign was based on topographical maps (1:10,000) and high resolution aerial photographs (nominal spatial resolution 0.4 m). The land use maps were used for subsequent calculations of landscape metrics with the software FRAGSTATS 3.3 (McGarigal *et al.* 2002).

To test whether landscape heterogeneity affects foraging trip duration, we calculated two metrics of landscape composition (percentage semi-natural habitat, Shannon's Diversity of land use types) and one metric of landscape configuration (Shape Index). All landscape metrics were calculated for eight different spatial scales that were represented by circular landscape sectors with radii of 250 m, 500 m, 750 m, 1,000 m, 1,250 m, 1,500 m, 1,750 m and 2,000 m around the centre of the study site.

The Shape Index was calculated as the median ratio of a patch perimeter divided by the perimeter of a maximally compact patch (i.e. a square) of the corresponding area. In contrast to the Perimeter-Area-Ratio, it corrects for the confounding effect of patch size (McGarigal *et al.* 2002). A Shape Index of one indicates that all habitat patches within a landscape are maximally compact, while higher values reflect increasingly complex shapes of habitats with higher amounts of habitat edges. Hence, the Shape Index indicates spatial complexity of landscapes.

Local land use intensity on the grassland study site was assessed by a compound, additive index called 'Land Use Intensity Index' (LUI) (Fischer *et al.* 2010; Bluethgen *et al.* 2012). It integrates grazing intensity, mowing frequency and fertilizer input for each study site.

6.3.3 Foraging flight efficiency

We started with observations of foraging flights five days after installation of hibernation boxes during good weather conditions. Observations of foraging activity were restricted to the following conditions: above 14°C, no clouds and a wind force of not more than 3 Beaufort-Scale, i.e. leaves and small branches move. We marked the nest entrance with a solvent-free touch-up pen ('uni PAINT Marker', Bienenzuchtbedarf Seip, Butzbach) to observe individual females for one hour without disturbing them by direct marking. Females are generally attached to their nests if they are not disturbed by other females (personal observation). The duration of foraging trips was measured with a stopwatch. In addition to foraging trip durations we also measured other nest-building activities: trips for loam, partition building, deposition of pollen, deposition of nectar and oviposition (Bosch & Vicens 2005). We observed a total of 111 individuals during three observation periods in the Alb, and during two observation periods in the Hainich (due to unfavorable weather conditions).

6.3.4 Measurement of reproductive success

After a diapause of five month, we dissected the nests to record the number of brood cells, parasitized cells, cells without content due to predation and cells with dead offspring (Gathmann & Tscharntke 1999). We also recorded the sex of the offspring and weighted the cocoons with a micro scales (Sartorius BL 150 S). The total offspring biomass per nest was calculated as (((proportion female offspring x mean weight of female offspring) + (proportion of male offspring x mean weight of male offspring))/100) x brood cell number per nest. The sex ratio per nest was calculated by dividing the number of female offspring by the sum of male and female offspring, multiplied by 100. The proportional weight of female cocoons per nest was calculated as the weight of female cocoons divided by the weight sum of male and female cocoons, multiplied by 100. The parasitism rate per nest was calculated as the percentage of parasitized or eaten brood cells, while mortality rate represents the percentage of brood cells per nest with unknown cause of death.

6.3.5 Statistical analyses

We used the software R 2.14.0 for Windows (R Development Core Team 2012) for statistical analyses. For each plot in each region several observations on multiple bee individuals were conducted. To account for the hierarchical structure in the data, we used general linear mixed effects models including a random term region (2)/ plot (18)/ survey (46) (lme, nlme package) (Pinheiro et al. 2011). We tested the influence of local and landscape variables on the duration of foraging trips by including temperature and LUI as fixed effects as well as landscape metrics of one scale. To estimate the spatial scale which had the largest effect on the duration of foraging trips, the full model was simplified for each spatial scale separately. As response, we calculated median values of foraging trip duration per bee. Then, model evaluation, based on Akaike Information Criterion, was performed to simplify the full model at each spatial scale. We used the 'dredge' function (R package 'MuMIn') to compare all possible models, including the null model. The models with the lowest AICc values were selected as final models (Burnham & Anderson 2004). We ln-transformed the foraging trip duration to adjust for heteroscedasticity and to gain a normal distribution of the residuals. Following (Kissling & Carl 2008), absence of spatial autocorrelation was verified based on Moran's I values for distance classes between 1 and 10 km.

Reproductive success was measured at two different levels: at the level of nests (number of brood cells, total offspring biomass, percentage of female offspring, percentage weight of female cocoons, parasitism rate and mortality rate) and at the level of plots (number of nests) was estimated at plot level. We used a linear model to correlate the nest number against the median duration of foraging trips per plot to test whether trip duration is related to reproductive success. For analyses on nest level, we performed general linear mixed effects models using plot nested in region as random term and median duration of foraging trips as fixed factor. To avoid heteroscedasticity and to fulfil the assumption of normality of residuals, we ln-transformed number of nests, square-root transformed the total offspring biomass and arcsine square-root transformed the percentage of female brood cells (Crawley 2007). Moreover, we applied variance functions in the model to deal with heterogeneity of variances (Zuur *et al.* 2009). A minimum-adequate model (including the null model) was again selected based on the Akaike Information Criterion (AICc) for model evaluation.

We checked for covariance among explanatory variables and found variance inflation factors < 3 and Pearson correlation coefficients < 0.65 which justified their simultaneous use in the models (Zuur *et al.* 2009, 2010).

6.4 RESULTS

We observed the following trip durations of different numbers of bees: Median duration of loam trips was 181 s (16 bees), of constructing a partition 102 s (13 bees), of pollen-nectar trips 774 s (111 bees), of pollen deposition 43 s (108 bees), of nectar deposition 38 s (108 bees) and of oviposition 62 s (14 bees). Foraging for pollen and nectar was the most time consuming nest building activity (Fig. 17). Nest-building activities differed significantly between duration of pollen-nectar trips and any other activity (Tukey's HSD at $p < 0.05$). An increase in median duration of pollen-nectar trips per plot was not associated with a changed duration of any other nest-building activity.

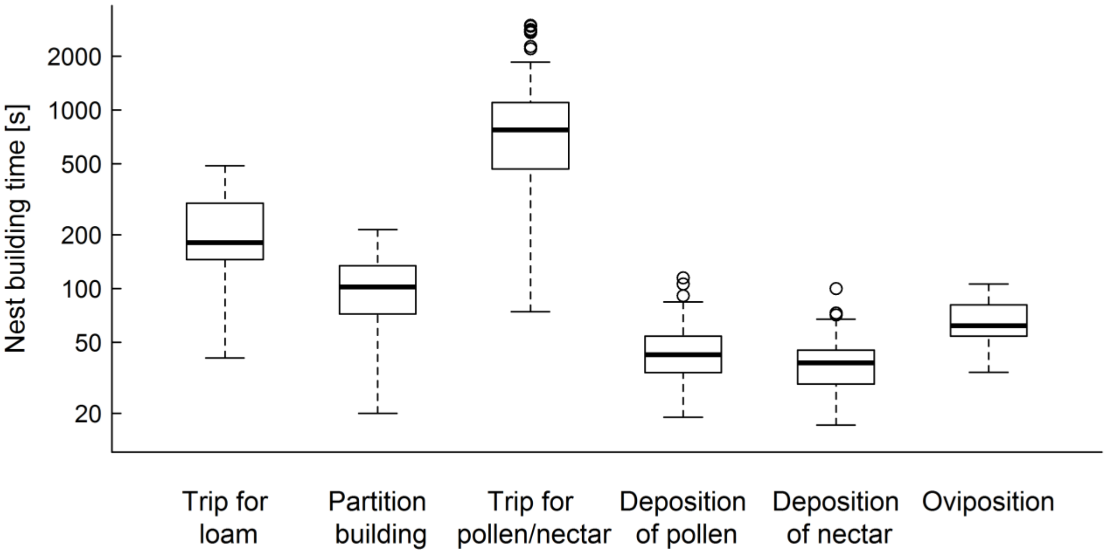

Figure 17 Time effort for foraging and other nest-building activities of *Osmia bicornis*. Boxplots show the median, interquartile range, minimum, maximum and outliers of six different activities. Values are shown on a ln-transformed y-axis.

The majority of variation in the duration of pollen-nectar trips was expressed in differences within individual bees (39.59 %), followed by differences between bees (37.98 %) and plots (14.04 %).

We found that landscape metrics at a scale of 1,250 m radius were most predictive in explaining foraging trip durations of bees (Fig. 18, Tab. 10).

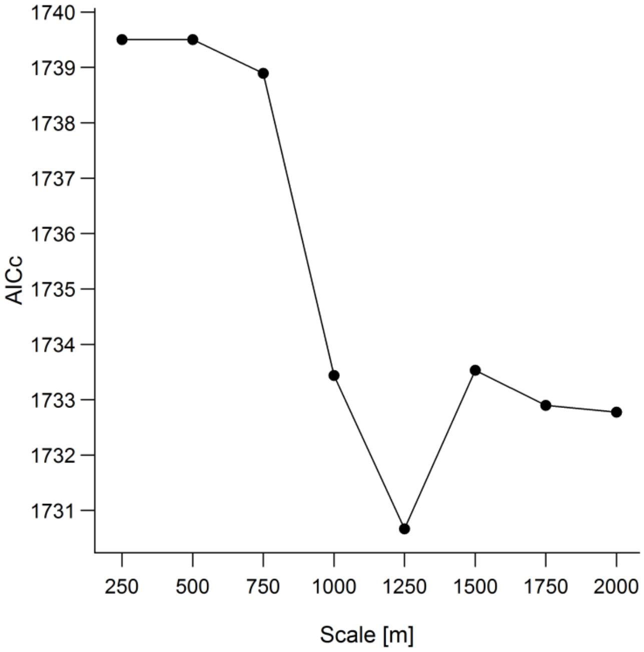

Figure 18 Effects of spatial scale on the explanatory value of landscape metrics for foraging time. The full model includes LUI, temperature, SHDI, SHAPE and % SNH and was simplified for each spatial scale. AICc values of the final model for each spatial scale that was best supported by the data are shown.

Table 10 Results of mixed effects model testing for potential relationships of ln-transformed foraging trips [s] and Land use intensity Index (LUI), flower cover [cm2], temperature [°C], Shannon's Diversity Index (SHDI), the median of the Shape Index (SHAPE) and the percentage of semi-natural habitats (% SNH) on a scale of 1250 m (N = 111 bees). Signif. codes: P < 0.001:***, P < 0.01: **, P < 0.05: *

	Full model					**Final model**				
Source of variation	numDF	denDF	F	P		numDF	denDF	F	P	
Intercept	1	64	4452.69	< 0.001	***	1	64	4767.47	< 0.001	***
LUI	1	11	0.41	0.5375		-	-	-	-	
Floco	1	11	0.31	0.5900		-	-	-	-	
Temperature	1	64	5.54	0.0217	*	1	64	6.64	0.0123	*
SHDI	1	11	0.64	0.4409		-	-	-	-	
SHAPE	1	11	6.61	0.0260	*	1	15	8.73	0.0098	**
% SNH	1	11	0.29	0.6039		-	-	-	-	

We observed significantly shorter foraging trips in complex landscapes showing high values of landscape configuration (high Shape indices) (Fig. 19). Foraging trips were neither affected by landscape composition (SHDI, % SNH), nor local management intensity, nor local flower cover (Tab. 10).

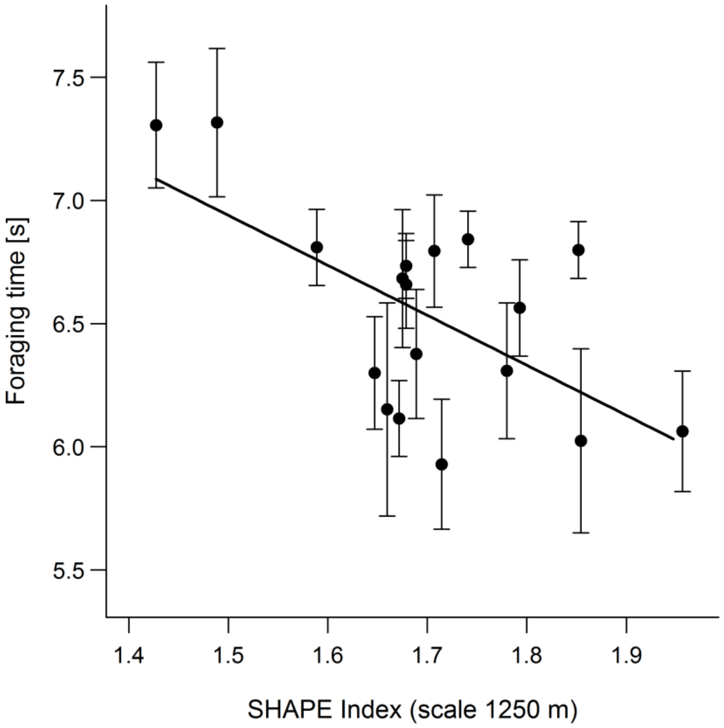

Figure 19 Mean pollen-nectar trip durations (ln-transformed) (± SE) in relation to spatial landscape complexity (Shape Index). For statistics see Table 10.

A total of 975 nests were counted, with 5,156 individual brood cells resulting in an average of 5.3 cells per nest. Calculating medians resulted in a total offspring biomass of 0.6 g per nest, an overall percentage of 51.79 female brood cells, a total parasitism rate of 0.9 % and a total mortality rate of 8.04 %. In contrast to our hypotheses, shorter foraging trips did not translate into enhanced reproductive success in terms of number of nest or brood cells, total offspring biomass, % female brood cells and % female weight (Tab. 11). Neither parasitism rate nor unexplained mortality rate were correlated with the duration of foraging trips (Tab. 11).

Table 11 Linear (mixed effects) models describing the effect of the median duration of pollen-nectar trips on fitness variables.

Source of variation	numDF	denDF	F	P
Number of brood cells				
(Intercept)	1	957	117.17	< 0.0001
Foraging time	1	15	0.28	0.6023
Percentage female offspring				
(Intercept)	1	845	256.86	< 0.0001
Foraging time	1	15	0.33	0.5731
Percentage female weight				
(Intercept)	1	841	435.93	< 0.0001
Foraging time	1	15	0.28	0.6043
Total offspring biomass				
(Intercept)	1	481	1212.25	< 0.0001
Foraging time	1	15	0.38	0.5489
Mortality rate				
(Intercept)	1	957	5.97	0.0147
Foraging time	1	15	4.44	0.0524
Parasitism rate				
(Intercept)	1	957	30.61	< 0.0001
Foraging time	1	15	0.74	0.4022

Source of variation	denDF	F	P
Number of nests			
Foraging time	1	0.00	0.9904
Residuals	16		

6.5 DISCUSSION

6.5.1 Landscape configuration & scales

Our study demonstrates that landscape configuration, i.e. the spatial complexity of different land use types determines the foraging efficiency of *O. bicornis* and not local habitat characteristics (Gimona *et al.* 2009). One possible reason why this bee was faster in nest provisioning in landscapes with a spatially complex configuration of land use patches is that foraging habitats are better connected and offer landmarks for orientation (Fauria, Campan & Grimal 2004). This may be of special importance under the light of long foraging flights to distant food resources that depend on orientation skills (Vicens & Bosch 2000). An increased compositional heterogeneity on the other hand was not sufficient to reduce the time needed to forage for pollen and nectar. Thus, too many different land use types within a foraging range, that also include habitats without food resources for wild bees (like forest, road and water bodies) could even prolong foraging flights. However, focussing on solitary bee richness and abundance, other studies demonstrated beneficial effects of landscape composition (measured as proportion of non-crop habitats) instead of configuration (edge density) (Holzschuh *et al.* 2010).

Shape complexity indices indicate an increased border length among different land-use types (Fahrig *et al.* 2011). Transition zones (forest-grassland, forest-crop field) have been discussed as ecotones, ecoclines and edges that might harbour higher plant species richness than the centre of habitats (Ries *et al.* 2004; Dabrowska-Prot & Wasilowska 2012). Since landscape diversity showed no effect on foraging efficiency, but spatial complexity of landscape elements and edges did, we assume a benefit for *O. bicornis* due to enhanced plant species richness and abundance in edges (Gathmann & Tscharntke 2002; Williams & Kremen 2007; Jha & Kremen 2013) in combination with an improved flight directionality (Vicens & Bosch 2000; Fauria *et al.* 2004).

Though, translocation experiments with *O. bicornis* gained a maximum foraging distance of 600 m (Gathmann 1998), we indirectly estimated a larger scale of 1,250 m at which *O. bicornis* perceives structural elements within its environment. This foraging range could be confirmed by personal observations of a marked bee from a neighbouring plot that bridged a distance of more than 2.5 km. Moreover, it could be shown for three trap-nesting bee species that their maximum foraging distances have been underestimated, ranging from 1.1 to 1.4 km, depending on their size (Zurbuchen *et al.* 2010b). This is in accordance with our results and supports our assumption that *O. bicornis* may increase foraging ranges to levels of > 1 km. However, this long distance may only apply to a small amount of single dispersers (Maddocks & Paulus 1987; Vicens & Bosch 2000). Two solitary bee species for instance stopped to forage at distances of 36 % and 50 % of their maximum foraging range (Zurbuchen *et al.* 2010b). Due to these individual differences and the predictive power of the Shape Index for foraging trips, we conclude that structural elements within landscape are crucial for orientation and that the size of foraging ranges may be highly depending on the specific spatial and temporal context.

6.5.2 Local land use intensity and resource abundance

Neither local management practices, like mowing, grazing or fertilizing, nor local flower cover significantly affected median duration of foraging trips of *O. bicornis* though it could earlier be shown that foraging trips were influenced by local food availability (Gathmann & Tscharntke 2002). In this study, we focused on managed grasslands that appartently do not offer sufficient food plant resources for *O. bicornis*. In contrast, other studies showed that flower-rich calcareous grasslands and orchards represent important foraging habitats (Gathmann & Tscharntke 1999, 2002). Despite short flowering times, mass flowering crops like oilseed rape could also enhance the reproductive success (Jauker *et al.* 2012; Holzschuh *et al.* 2012). Our results show that deficient food resources on managed grasslands can be compensated by structurally complex landscapes with connecting corridors and landmarks.

6.5.3 Nest building activity

Regarding all nest building activities, bees needed most of their time budget to forage for pollen and nectar (Fig. 1) (Maddocks & Paulus 1987; Rathjen 1994). Longer foraging times could not be compensated by reduced time allocation into necessary other nest-building activities like the construction of a partition. The great variation in individual foraging trips confirms former results (Maddocks & Paulus 1987). Since we observed one and the same bee in similar microclimatic conditions (cloudiness, temperature) (Strohm *et al.* 2002; Klein *et al.* 2004), other factors, such as individual weight, health or orientation skills might have influenced the individual capability to exploit a food resource (Vicens & Bosch 2000).

6.5.4 Reproductive success

However, increased foraging efficiency did not increase the reproductive success. Longer foraging trips did not translate to a reduction in the reproductive success of *O. bicornis*, neither in brood cell numbers, nest abundance, mean offspring weight or sex ratios. In this study, we recorded total amounts of nests and brood cells constructed per study site, but we could not relate observed foraging trips of individual bees to total offspring brood cell numbers per female. Since the duration of individual foraging trips can vary strongly, we assume that an individual assignment of trips and brood cell/ nest numbers might yield more accurate results, especially if foraging trips can be associated with other nest-building activities of one and the same bee. We expected that the investment in sons would increase with longer foraging trips, since it has been shown that provisioning of daughters of the solitary bee *C. persimilis* is more costly: They always received three trips of pollen, sons mostly received two (Danforth 1990). Moreover, longer flight distances changed the sex ratio in favour of males (Peterson & Roitberg 2006a). However, we could not confirm these results, suggesting that other factors than foraging efficiency (e.g. food quality or infections) caused significant variation in the reproductive success of *O. bicornis*. Contrary to a former study, we could not confirm that the provisioning time per cell and risk of open cell parasitism were positively correlated (Seidelmann 2006).

6.6 CONCLUSIONS

We conclude that agricultural intensification at local scale might not be sufficient to explain time patterns of foraging trips but might lead to wrong conclusions if the landscape context of a site is not accounted for (Tscharntke *et al.* 2005; Concepcion *et al.* 2012). The spatial configuration of landscapes was mainly driving the foraging efficiency of *O. bicornis* whereas landscape composition or local land use intensity did not show any effects. Edge structures presumably served as corridors, harbouring a high number of food plant species and providing edge structures for orientation. Although, local flower cover failed to explain patterns of foraging trip durations, conservation and management schemes should promote an extensive land use at local scale to maintain local pollen and nectar resources (Gathmann & Tscharntke 2002) and to reduce disturbances of bees (Winfree *et al.* 2009).

Depending on species mobility, studies should include local as well as larger spatial scales (Tscharntke *et al.* 2005; Greenleaf *et al.* 2007). Importantly, landscape composition and configuration can differently affect foraging trips, species diversity and abundances (Gimona *et al.* 2009; Fahrig *et al.* 2011) and should therefore be distinguished and accounted for. We conclude that foraging efficiency of solitary bees can be enhanced by spatially complex landscapes. Thus, future agri-environment schemes should also consider the shape and spatial arrangement of agricultural habitats and promote edge structures such as hedges, sown flower strips, field margins and other connecting habitat elements.

6.7 APPENDIX

Table A8 Plot coordinates of the study plots in 2009

Plot	Longitude	Latitude
HEG07	10.410398510	51.27357932
HEG15	10.486213180	51.06803131
HEG22	10.324907910	51.03077098
HEG31	10.221174330	51.17037600
HEG38	10.341794030	51.11640425
HEG40	10.446796600	50.96680908
HEG41	10.366680670	51.22104132
HEG48	10.380115710	51.28685018
AEG01	9.341986753	48.39800501
AEG03	9.532378750	48.40888149
AEG06	9.441678107	48.40126215
AEG09	9.502801818	48.39467225
AEG11	9.347715524	48.48539880
AEG15	9.448656586	48.48725377
AEG21	9.357227747	48.44220468
AEG25	9.259596583	48.39547800
AEG26	9.403881830	48.39510617
AEG35	9.288446518	48.48088728

7 CHAPTER V

General discussion

We conducted this thesis to examine land use effects across spatial scales on a complex study system involving interacting species groups of different trophic levels. The species groups involved, namely cavity-nesting bees and wasps and their antagonists, require different resources and exhibit different species traits. Hence, the studied factors at local and landscape scales likely affect these interacting groups differently and thus shape their biotic interactions and their ecosystem services in different directions.

7.1 SPECIES INTERACTIONS ON LOCAL LAND USE (CHAPTER II)

To gain insight into how system dependent interactions are affected by local land use, we manipulated vegetation structure by mowing small plots within regularly managed grasslands. Most brood cells were attacked by flying antagonists on mown plots within regularly mown grassland sites. Similarly, ground-dwelling antagonists counteracted flying antagonists most effectively on mown plots within mown grasslands. In contrast, high vegetation on unmown plots levelled out the success of flying antagonists, presumably by concealing host nests from flying antagonists. Moreover, no interactions between both antagonistic groups were visible on grazed or grazed & mown sites. Antagonistic interactions were most conspicuous on mown plots within mown grassland sites, pointing to a facilitated meeting of prey and predators or hosts and parasitoids in simple structured vegetation (Gingras *et al.* 2002; Sanders *et al.* 2008). Higher vegetation on the other hand might offer more abundant prey species for ground-dwellers. Generally, ground-dwelling antagonists did not affect the colonisation success of bees and wasps but displaced their flying antagonists on mown plots, presumably through visual or chemical cues (Dicke & Grostal 2001). Colonization success of bees and wasps was less affected by small-scaled manipulations of vegetation structure but best supported on grazed sites, whereas biotic interactions between flying and ground-dwelling antagonists were modulated by vegetation structure.

7.2 LANDSCAPE EFFECTS (CHAPTER III)

As soon as landscape metrics of up to 2,000 m were involved in our studies, these landscape metrics were more predictive in explaining species richness, abundance and biotic interactions than local metrics. This is in accordance with other insect studies that found management systems to be less influential than landscape structures (Weibull *et al.* 2000; Fahrig *et al.* 2011; Tscharntke *et al.* 2012). Diverse landscapes within 250 m around the nests enhanced host richness and abundance, whereas spatial complex structured landscapes within 1,500 m favoured their antagonists. This large scale might be a response of antagonists to spatial and temporal fluctuations in host populations (Thies *et al.* 2003) causing food resource gaps. These local resource gaps for hosts and their flying antagonists can be compensated by a heterogeneous landscape. As hypothesized, the hosts and their antagonists were differently promoted by landscape heterogeneity. The requirements of hosts were accounted for by landscape diversity. Multiple habitats may easily cover their needs for food and nesting resources. However, their antagonists depend on floral rich habitats that simultaneously offer resources for their host species (Albrecht *et al.* 2007). Habitat edges provide a higher plant species richness than the centre (Ries *et al.* 2004; Dabrowska-Prot & Wasilowska 2012) and can facilitate dispersal through connecting landmarks and corridors. Our results are consistent with a former study that found antagonists to rely more than their hosts on connected habitats to rotate if necessary (Tscharntke & Kruess 1999).

Against our hypothesis, the local Land Use Index (LUI) only played a marginal role for hosts. However, antagonists were most abundant at high flower diversity, which promotes food and shelter for predators, parasitoids and pollinators (Westrich 1989).

7.3 FORAGING SUCCESS (CHAPTER IV)

Similarly, neither the LUI nor local flower cover affected the foraging success of the Red Mason Bee, contrary to a former study (Gathmann & Tscharntke 2002). Again, we analysed local as well as landscape effects on the foraging and reproductive success of *O. bicornis.* In particular, we showed that spatially complex landscapes enhanced the foraging efficiency of *O. bicornis.* Complex landscapes connect foraging habitats, offer landmarks for orientation (Tinbergen 1984; Vicens & Bosch 2000; Fauria *et al.* 2004) and bear habitat edges of high plant species richness and abundance (Gathmann & Tscharntke 2002; Williams & Kremen 2007; Jha & Kremen 2013). Therefore, bees are faster and more effective in foraging for pollen and nectar in spatially complex landscapes.

However, landscape diversity, measured as the composition of differing land use types, did not correlate with the foraging efficiency of the Red Mason Bee. We assume a disadvantage of too many different land use types within foraging ranges, because land use types also included resource-poor or disturbed types like forests, roads and water bodies.

7.4 REPRODUCTIVE SUCCESS (CHAPTER IV)

The reproductive success of the Red Mason Bee (*Osmia bicornis*), measured as brood cell numbers, nest abundance, mean offspring weight or sex ratios, was not related to foraging efficiency as hypothesized. Longer foraging trips should increase the investment in the least costly sex (sons) as shown for larger flight distances (Peterson & Roitberg 2006a). For instance, sons of the solitary bee *C. persimilis* mostly received two, whereas daughters always received three pollen trips (Danforth 1990). We assume that besides foraging trip durations other factors that we did not account for like the mix and quality of pollen and nectar or deceases and infections (mould, mites, etc.) are also important in determining the reproductive success of the Red Mason Bee.

7.5 SPECIES TRAITS (CHAPTER II & CHAPTER IV)

We did observe that the affinity of being attacked by flying antagonists depended not only on the type of closure that a nest had but also on the local abundance of a nest closure type and the associated number of antagonist species. In other words, the attack rate was negatively density dependent. The more nests of a certain closure type occurred the lower was the attack rate. The nest closure represents a shield against predators, parasites and parasitoids (Krombein 1967). We found that nests closed by a membrane were least attacked, in contrast to leaf slice-nests, which were more frequently attacked. Further, attack rates of each closure type decreased with increasing nest abundance and increased with increasing number of associated antagonist species. Resulting advantages from nest aggregations might be a better defence against antagonists through a more effective parasite detection, parasite confusion or active group defence (Rosenheim 1990). Closures made of leaf-slices may be more protective than those made of membrane but resulted in a higher attack rate presumably due to the higher number of associated antagonist species (at similar local nest abundance)(cf. Tab. A3).

The median time needed by *Osmia bicornis* to collect loam for constructing a partition was 4 min. and 10 s (cf. Fig. 17). However, most of the time was spent on pollen and nectar foraging (15 min. and 6 s), which is in accordance with former studies, just like highly varying individual foraging trips (40 % of the total variation) (Maddocks & Paulus 1987; Rathjen 1994). This high variance might be caused by individual orientation skills, weight or health (Tinbergen 1984; Vicens & Bosch 2000) and represents the individual potential to efficiently collect food for the brood. Furthermore, we observed that longer foraging trips of *O. bicornis* do not result in a shorter time spent for nest construction.

7.6 CONCLUSIONS

To meet human nutritional needs, ongoing intensification of agricultural practices shaped a uniform appearance of our landscapes. Similarly, essential ecosystem services, like crop pollination and pest control, suffer from these land use changes. Species diversity of bees and plants that they pollinate are declining (Biesmeijer et al. 2006), because bees rely on nesting resources and flowering plants within limited ranges around the nests (Gathmann & Tscharntke 2002; Greenleaf *et al.* 2007). These requirements cannot be met within homogeneous, less diverse landscapes. In contrast, grassland management that promotes high habitat heterogeneity can benefit bees and wasps (Schaich & Barthelmes 2012) and thus pollination and pest control services.

In this large-scaled and highly replicated field study, we were able to reveal dependencies of functional biodiversity on land use effects by comprehensive monitoring, manipulations of grassland management and exclusion experiments. Our grassland experiments revealed that above-ground nesting solitary bees and wasps were preferably attacked by flying and ground-dwelling antagonists on mown grasslands. Host-attacks of flying antagonists were most effectively counteracted by ground-dwelling arthropods on mown sites whereas high vegetation modulated their interaction. Furthermore, the risk of parasitism depended on nest closure types, nest closure abundances and the associated number of antagonist species.

The monitoring of hosts and their antagonists in different landscapes resulted in distinct responses to landscape metrics. Host species required high landscape diversity and antagonists benefitted from spatially complex landscape. Taking into account the different dispersal abilities and home ranges of species, hosts responded to smaller spatial scales than their antagonists. Thus ecosystem services like pollination and predation by hosts can be maintained by arranging multiple different habitats within small ranges (cf. Ricketts *et al.* 2008). Their antagonists, regulating (pest) populations, required high host abundance and thus host-habitat connecting elements at large spatial scales.

The foraging efficiency of *O. bicornis* was mainly shaped by the spatial complexity of landscape. Thus, landscapes with high amounts of edges, field margins and corridors between foraging habitats can benefit solitary bees by providing abundant floral resources.

The species that we studied represented very heterogeneous groups of important indicator taxa of ecological function with different habitat requirements and species traits. They provided unambiguous and significant responses to different local and landscape metrics. Foraging trips, for instance, were driven by landscape configuration. We conclude that a heterogeneous arrangement of habitats, differing in vegetation structure, can promote a diversity of interacting species groups. Similarly, the spatial scales of influential metrics depend on species-specific dispersal and foraging ranges. Therefore, management schemes should consider local measures, like fallow strips, corridors and hedges, which connect a multitude of different habitats at the landscape scale and thus promote landscape diversity and spatial structure.

The core of the results gained from our studies is that local as well as large scale effects of land use contribute to the responses of all species groups. The decisive difference is which metrics are used to measure land use effects and which spatial scales are involved. Thus, future studies should involve local and landscape metrics and account for species-specific spatial scales.

8 REFERENCES

Adler, P.B., Raff, D.A. & Lauenroth, W.K. (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia*, **128**, 465–479.

Albrecht, M., Duelli, P., Schmid, B. & Müller, C.B. (2007) Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *Journal of Animal Ecology*, **76**, 1015–1025.

Barthell, J.F., Frankie, G.W. & Thorp, R.W. (1998) Invader Effects in a Community of Cavity Nesting Megachilid Bees (Hymenoptera: Megachilidae). *Environmental Entomology*, **27**, 240–247.

Batista Matos, M.C., Sousa-Souto, L., Almeida, R.S. & Teodoro, A.V. (2013) Contrasting Patterns of Species Richness and Composition of Solitary Wasps and Bees (Insecta: Hymenoptera) According to Land-use. *Biotropica*, **45**, 73–79.

Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 485–488.

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemueller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Bivand, R. (2012) spdep: Spatial dependence: weighting schemes, statistics and models. URL http://cran.r-project.org/

Bluethgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., Hoelzel, N., Alt, F., Boch, S., Gockel, S., Hemp, A., Mueller, J., Nieschulze, J., Renner, S.C., Schoening, I., Schumacher, U., Socher, S.A., Wells, K., Birkhofer, K., Buscot, F., Oelmann, Y., Rothenwoehrer, C., Scherber, C., Tscharntke, T., Weiner, C.N., Fischer, M., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D. & Weisser, W.W. (2012) A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology*, **13**, 207–220.

Borer, E.T., Seabloom, E.W. & Tilman, D. (2012) Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters*, **15**, 1457–1464.

Bosch, J. & Vicens, N. (2005) Sex allocation in the solitary bee Osmia cornuta: do females behave in agreement with Fisher's theory? *Behavioral Ecology and Sociobiology*, **59**, 124–132.

Brose, U. (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, **135**, 407–413.

Brueckmann, S.V., Krauss, J., van Achterberg, C. & Steffan-Dewenter, I. (2011) The impact of habitat fragmentation on trophic interactions of the monophagous butterfly *Polyommatus coridon*. *Journal of Insect Conservation*, **15**, 707–714.

Burnham, K. & Anderson, D. (2004) Multimodel inference - understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.

Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J. & Kremen, C. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, **14**, 922–932.

Concepcion, E.D., Diaz, M., Kleijn, D., Baldi, A., Batary, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh, A., Knop, E., Marshall, E.J.P., Tscharntke, T. & Verhulst, J. (2012) Interactive effects of landscape context constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, **49**, 695–705.

Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex PO19 8SQ, England.

Dabrowska-Prot, E. & Wasilowska, A. (2012) The Role of Ecotones in Man-Disturbed Landscape: Boundaries Between Mixed Forest and Adjacent Man-Made Ecosystems in the Kampinos National Park, Poland. *Polish Journal of Ecology*, **60**, 677–698.

Danforth, B.N. (1990) Provisioning behavior and the estimation of investment ratios in a solitary bee *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behavioral Ecology and Sociobiology*, **27**, 159–168.

Dennis, P. (2003) Sensitivity of upland arthropod diversity to livestock grazing, vegetation structure and landform.

Dicke, M. & Grostal, P. (2001) Chemical detection of natural enemies by arthropods: an ecological perspective. *Annual Review of Ecology and Systematics*, 1–23.

Durrer, S. & Schmid-Hempel, P. (1995) Parasites and the regional distribution of bumblebee species. *Ecography*, **18**, 114–122.

Ebeling, A., Klein, A.-M., Weisser, W.W. & Tscharntke, T. (2012) Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia*, **169**, 453–465.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, **14**, 101–112.

Fauria, K., Campan, R. & Grimal, A. (2004) Visual marks learned by the solitary bee *Megachile rotundata* for localizing its nest. *Animal Behaviour*, **67**, 523–530.

Fischer, M., Bossdorf, O., Gockel, S., Haensel, F., Hemp, A., Hessenmoeller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schoening, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D. & Weisser, W.W. (2010) Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, **11**, 473–485.

Ford, H., Garbutt, A., Jones, L. & Jones, D.L. (2013) Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect Conservation and Diversity*, **6**, 189–200.

Forman, R.T.T. (1995) Some general principles of landscape and regional ecology. *Landscape Ecology*, **10**, 133–142.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Gathmann, A. (1998) *Bienen, Wespen Und Ihre Gegenspieler in Der Agrarlandschaft: Artenreichtum Und Interaktionen in Nisthilfen, Habitatbewertung Und Aktionsradien*. University of Göttingen.

Gathmann, A., Greiler, H.-J. & Tscharntke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia*, **98**, 8–14.

Gathmann, A. & Tscharntke, T. (1999) Landschafts-Bewertung mit Bienen und Wespen in Nisthilfen: Artenspektrum, Interaktionen und Bestimmungsschlüssel. *Naturschutz und Landschaftspflege Baden-Württemberg*, **73**, 277–305.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology, Journal of Animal Ecology*, **71**, 757–764.

Gimona, A., Messager, P. & Occhi, M. (2009) CORINE-based landscape indices weakly correlate with plant species richness in a northern European landscape transect. *Landscape Ecology*, **24**, 53–64.

Gingras, D., Dutilleul, P. & Boivin, G. (2002) Modeling the impact of plant structure on host-finding behavior of parasitoids. *Oecologia*, **130**, 396–402.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Helden, A.J., Anderson, A., Sheridan, H. & Purvis, G. (2010) The role of grassland sward islets in the distribution of arthropods in cattle pastures. *Insect Conservation and Diversity*, **3**, 291–301.

Hendrickx, F., Maelfait, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekoetter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V. & Bugter, R. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, **44**, 340–351.

Holland, J.D., Bert, D.G. & Fahrig, L. (2004) Determining the spatial scale of species' response to habitat. *Bioscience*, **54**, 227–233.

Holt, R.D. (1996) *Food Webs in Space: An Island Biogeographic Perspective* (eds GA Polis and KO Winemiller). Chapman & Hall, New York, USA.

Holt, R.D., Lawton, J.H., Polis, G.A. & Martinez, N.D. (1999) Trophic rank and the species-area relationship. *Ecology*, **80**, 1495–1504.

Holzschuh, A., Dormann, C.F., Tscharntke, T. & Steffan-Dewenter, I. (2012) Mass-flowering crops enhance wild bee abundance. *Oecologia*.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, T. (2007a) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D. & Tscharntke, T. (2007b) Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, **44**, 41–49.

Holzschuh, A., Steffan-Dewenter, I. & Tscharntke, T. (2010) How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, **79**, 491–500.

Hudewenz, A., Klein, A.-M., Scherber, C., Stanke, L., Tscharntke, T., Vogel, A., Weigelt, A., Weisser, W.W. & Ebeling, A. (2012) Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. *Biological Conservation*, **150**, 42–52.

Humbert, J.-Y., Ghazoul, J. & Walter, T. (2009) Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems & Environment*, **130**, 1–8.

Jauker, F., Peter, F., Wolters, V. & Diekötter, T. (2012) Early reproductive benefits of mass-flowering crops to the solitary bee Osmia rufa outbalance post-flowering disadvantages. *Basic and Applied Ecology*.

Jha, S. & Kremen, C. (2013) Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences*, **110**, 555–558.

Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. & Daily, G.C. (2012) Intensive agriculture erodes β-diversity at large scales. *Ecology Letters*, **15**, 963–970.

Kissling, W.D. & Carl, G. (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, **17**, 59–71.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004) Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology*, **73**, 517–525.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, **99**, 16812–16816.

Krombein, K.V. (1967) *Trap-nesting Wasps and Bees: Life Histories, Nests and Associates*. Smithonian Press, Washington, District of Colombia.

Kruess, A. (2003) Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography*, **26**, 283–290.

Kruess, A. & Tscharntke, T. (1994) Habitat fragmentation, species loss and biological control. *Science*, **264**, 1581–1584.

Lack, D. (1969) The numbers of bird species on islands. *Bird study*, **16**, 193–209.

Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005) Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions*, **11**, 73–82.

Li, H. & Reynolds, J.F. (1995) On definition and quantification of heterogeneity. *Oikos*, **73**, 280–284.

Maddocks, R. & Paulus, H., F. (1987) Quantitative aspects of the breeding biology of *Osmia rufa (L.)* and *Osmia cornuta (Latr.)* (Hymenoptera, Megachilidae): A comparative study of competition-reducing mechanisms in 2 closely related bee species. *Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere*, **114**, 15–44.

McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.

Noordijk, J., Delille, K., Schaffers, A.P. & Sýkora, K.V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, **142**, 2097–2103.

O'Neill, K.M. (2001) *Solitary Wasps: Behavior and Natural History*. Cornell University Press.

Peterson, J.H. & Roitberg, B.D. (2006a) Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee *Megachile rotundata*. *Behavioral Ecology and Sociobiology*, **59**, 589–596.

Peterson, J.H. & Roitberg, B.D. (2006b) Impact of resource levels on sex ratio and resource allocation in the solitary bee *Megachile rotundata*. *Environmental Entomology*, **35**, 1404–1410.

Pinheiro, J., Bates, D., Debroy, S., Sarkar, D. & the R Development Core Team. (2011) *Nlme: Linear and Nonlinear Mixed Effects Models.*

R Development Core Team. (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0

Rand, T.A., van Veen, F.J.F. & Tscharntke, T. (2012) Landscape complexity differentially benefits generalized fourth, over specialized third, trophic level natural enemies. *Ecography*, **35**, 97–104.

Rathjen, H. (1994) Neuere Aspekte zur Brutbiologie und zum Orientierungsvermögen von *Osmia rufa (L.)* (Hymenoptera, Megachilidae).

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A. & Viana, B.F. (2008) Landscape effects on crop pollination services: are there general patterns? *Ecology Letters*, **11**, 499–515.

Ries, L., Jr., R.J.F., Battin, J. & Sisk, T.D. (2004) Ecological Responses to Habitat Edges: Mechanisms, Models, and Variability Explained. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 491–522.

Rosenheim, J.A. (1990) Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Annals of the Entomological Society of America*, **83**, 277–286.

Rothenwoehrer, C., Tscharntke, T., Bellach, M., Steckel, J., Steffan-Dewenter, I., Westphal, C. & Scherber, C. Efficiency of insect conservation management on grasslands increases with local land use intensity.

Sanders, D., Nickel, H., Grützner, T. & Platner, C. (2008) Habitat structure mediates top–down effects of spiders and ants on herbivores. *Basic and Applied Ecology*, **9**, 152–160.

Schaich, H. & Barthelmes, B. (2012) Management of grasslands in rewetted floodplains: effects of grazing and cutting on vegetation development. *Tuexenia*, 207–231.

Seidelmann, K. (2006) Open-cell parasitism shapes maternal investment patterns in the Red Mason bee *Osmia rufa*. *Behavioral Ecology*, **17**, 839–848.

Seidelmann, K., Ulbrich, K. & Mielenz, N. (2010) Conditional sex allocation in the Red Mason bee *Osmia rufa* . *Behavioral Ecology and Sociobiology*, **64**, 337–347.

Shannon, C.E. & Weaver, W. (1949) *Mathematical Theory of Communication*. University of Illinois Press.

Socher, S.A., Prati, D., Boch, S., Mueller, J., Klaus, V.H., Hoelzel, N. & Fischer, M. (2012) Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology*, **100**, 1391–1399.

Sokal, R.R. & Rohlf, F.J. (1994) *Biometry: The Principles and Practices of Statistics in Biological Research*, 3rd ed. Palgrave Macmillan.

Steffan-Dewenter, I. (2002) Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology*, **27**, 631–637.

Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, **17**, 1036–1044.

Steffan-Dewenter, I. & Leschke, K. (2003) Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodiversity & Conservation*, **12**, 1953–1968.

Steffan-Dewenter, I. & Schiele, S. (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, **89**, 1375–1387.

Steffan-Dewenter, I. & Tscharntke, T. (2002) Insect communities and biotic interactions on fragmented calcareous grasslands—a mini review. *Biological Conservation*, **104**, 275–284.

Strohm, E., Daniels, H., Warmers, C. & Stoll, C. (2002) Nest provisioning and a possible cost of reproduction in the megachilid bee *Osmia rufa* studied by a new observation method. *Ethology Ecology & Evolution*, **14**, 255–268.

Swift, M.J., Izac, A.-M.N. & van Noordwijk, M. (2004) Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? *Agriculture, Ecosystems & Environment*, **104**, 113–134.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.

Thies, C., Roschewitz, I. & Tscharntke, T. (2005) The landscape context of cereal aphid–parasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 203–210.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18–25.

Tinbergen, N. (1984) *Curious Naturalists*, Revised. University of Massachusetts Press.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, **35**, 708–719.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.

Tscharntke, T. & Kruess, A. (1999) Habitat fragmentation and biological control. *Hawkins, B.A., Cornell, H.V. (Eds.), Theoretical approaches to biological control* pp. 190–205. Cambridge University Press, Cambridge.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fruend, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Tylianakis, J.M., Klein, A.M., Lozada, T. & Tscharntke, T. (2006) Spatial scale of observation affects alpha, beta and gamma diversity of cavity-nesting bees and wasps across a tropical land-use gradient. *Journal of Biogeography*, **33**, 1295–1304.

Ulbrich, K. & Seidelmann, K. (2001) Modeling population dynamics of solitary bees in relation to habitat quality. *Web Ecology*, **2**, 57–64.

Veddeler, D., Tylianakis, J., Tscharntke, T. & Klein, A.-M. (2010) Natural enemy diversity reduces temporal variability in wasp but not bee parasitism. *Oecologia*, **162**, 755–762.

Vicens, N. & Bosch, J. (2000) Nest Site Orientation and Relocation of Populations of the Orchard Pollinator Osmia cornuta (Hymenoptera: Megachilidae). *Environmental Entomology*, **29**, 69–75.

Warfe, D.M. & Barmuta, L.A. (2004) Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, **141**, 171–178.

Weibull, A., Bengtsson, J. & Nohlgren, E. (2000) Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, **23**, 743–750.

Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyoergyi, H., Tscheulin, T., Vaissiere, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J. & Steffan-Dewenter, I. (2008) Measuring bee diversity in different european habitats and biogeographical regions. *Ecological Monographs*, **78**, 653–671.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2006a) Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia*, **149**, 289–300.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2006b) Foraging trip duration of bumblebees in relation to landscape-wide resource availability. *Ecological Entomology*, **31**, 389–394.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2009) Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, **46**, 187–193.

Westrich, P. (1989) *Die Wildbienen Baden-Württembergs*. E. Ulmer, Stuttgart.

Westrich, P. (1996) The conservation of bees. *Habitat requirements of central European bees and the problems of partial habitats* Linnean Society Symposium Series. pp. 1–16. London (Academic Press).

Williams, N.M. & Kremen, C. (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, **17**, 910–921.

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. & Aizen, M.A. (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, **90**, 2068–2076.

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010a) Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology*, **79**, 674–681.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010b) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, **143**, 669–676.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer.

9 AUTHOR CONTRIBUTIONS

9.1 CHAPTER II

This chapter is yet to be submitted as

Steckel, J, Peters, MK, Westphal C, & Steffan-Dewenter, I (in prep.) **Habitat management mediates shifts in the impact of ground-dwelling and flying antagonists on solitary bees and wasps**

The work distribution among authors was as follows

JS, CW & ISD developed the experimental design. JS collected the data in the field, performed laboratory work and data management. JS and MKP analysed the data. All authors contributed to the interpretation of the results. JS wrote the first draft. All co-authors (MKP, CW & ISD) contributed to the final manuscript.

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offices of Baden-Wuerttemberg, Thueringen, and Brandenburg (according to § 72 BbgNatSchG).

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9.2 Chapter III

This chapter is yet to be submitted as

Steckel, J, Westphal C, Peters, MK, Bellach, M, Rothenwoehrer, C, Erasmi S, Scherber, C, Tscharntke, T & Steffan-Dewenter, I (in prep.) **Landscape composition and configuration differently affect trap-nesting bee and wasp hosts and their antagonists**

The work distribution among authors was as follows

JS, CW, MB, CR, CS, TT, ISD developed the experimental design. JS, MB, CR selected the study sites and collected the data in the field. JS performed laboratory work and data management. Landscape analysis was performed by JS, CW, MB, CR and SE.

JS and MKP analysed the data. JS, CW, MKP, ISD interpreted the results. JS wrote the manuscript, and all co-authors contributed to writing the final manuscript: CW, MKP, MB, CR, SE, CS, TT, ISD.

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9.3 CHAPTER IV

This chapter is yet to be submitted as

Steckel, J, Peters, MK, Westphal C, & Steffan-Dewenter, I (in prep.) **Spatially complex landscapes enhance the foraging efficiency of a solitary bee (*Osmia bicornis*)**

The work distribution among authors was as follows

JS, CW & ISD developed the experimental design. JS collected the data in the field, performed laboratory work and data management. JS and MKP analysed the data. All Authors contributed to the interpretation of the results. JS wrote the first draft of the manuscript and MKP, CW & ISD extensively revised the manuscript.

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10 PUBLICATION LIST

Steckel, J., Penrith, M. L., Henschel, J., Brandl, R. & Meyer, J. 2010 A preliminary molecular phylogeny of the Namib Desert darkling beetles (Tenebrionidae)

Steckel, J., Peters, M. K., Westphal, C. & Steffan-Dewenter, I., in prep., Habitat management mediates shifts in the impact of ground-dwelling and flying antagonists on solitary bees and wasps

Steckel, J., Westphal C., Peters, M. K., Bellach, M., Rothenwöhrer, C., Erasmi S., Scherber, C., Tscharntke, T. & Steffan-Dewenter, I., in prep., Landscape composition and configuration differently affect trap-nesting bee and wasp hosts and their antagonists

Steckel, J., Peters, M. K., Westphal, C. & Steffan-Dewenter, I., in prep., Spatially complex landscapes enhance the foraging efficiency of a solitary bee (*Osmia bicornis*)

Allan, E., Bossdorf, O., Dormann, C. F., Prati, D., Gossner, M., Blüthgen, N., Barto, K., Bellach, M., Birkhofer, K., Boch, S., Böhm, S., Börschig, C., Chatzinotas, A., Christ, S., Daniel, R., Diekötter, T., Fischer, C., Friedl, T., Glaser, K., Hallman, C., Hodaĉ, L., Hölzel, N., Jung, K., Klein, A.-M., Klaus, V., Kleinebecker, T., Krauss, J., Lange, M., Müller, J., Nacke, H., Pašalić, E., Rillig, M., Rothenwöhrer, C., Schall, P., Scherber, C., Schulze, W., Socher, S., **Steckel, J.**, Steffan-Dewenter, I., Türke, M., Tscharntke, T., Weiner, C., Werner, M., Westphal, C., Wolters, V., Wubet, T., Gockel, S., Gorke, M., Hemp, A., Renner, S. C., Schöning, I., Pfeiffer, S., König-Reis, B., Buscot, F, Linsenmair, K.-E., Schulze, E.-D., Weisser, W. W., Fischer, M., in prep., Inter-annual variation in land-use intensity enhances grassland multidiversity

Hancock, C., Arnold, S., Wäschke, N., Bellach, M., Meiners, T., Peters, M. K., Rothenwöhrer, C., **Steckel, J.**, Westphal, C., Obermaier, E., in prep., Landscape wide land use intensity determines local abundance of higher trophic levels in grassland habitats

Rothenwöhrer, C., Tscharntke, T., Bellach, M., **Steckel, J.**, Steffan-Dewenter, I., Westphal, C. & Scherber, C., submitted, Efficiency of insect conservation management on grasslands increases with local land use intensity

11 CURRICULUM VITAE

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Nationality	German

Education and Qualifications

April 2008 – September 2013	**PhD thesis** ‘*Effects of landscape heterogeneity and land use on interacting groups of solitary bees, wasps and their flying and ground-dwelling antagonists*’ at the *Department of Animal Ecology and Tropical Biology*, University of Würzburg (working group of I. Steffan-Dewenter)
December 2006 – December 2007	**Diploma thesis** ‘A phylogenetic approach to darkling beetles in the Namib desert based on molecular genetics’ at the *Department of Animal Ecology*, University of Marburg (wworking group of R. Brandl)

October 2001 – October 2006	**Studies in biology** at the University of Marburg, since 2003 with the major subjects Animal Ecology, Zoology and Nature Conservation
April 2005 – October 2005	**Practical course** in the *Department of Animal Ecology*: Morphometrical analysis of mandibles of ants
November 1998 – November 2000	**Studies** at the Akademie für Absatzwirtschaft Kassel, Certificate as ‚Kommunikationswirtin‘
June 1998	**A levels**, Theodor-Heuss-School, Homberg

Work experience

May 2003 – November 2007	**Student Assistant** in the working groups of *Animal Ecology* and *Nature Conservation,* Department of Biology, University of Marburg: image editing for lectures, administration of card indices of Heteroptera and Auchenorrhyncha, taxidermy of Heteroptera, Auchenorrhyncha and Isoptera
August 2002	**Internship** in the NABU-Water-Bird-Reservation, Wallnau: guidance of visitors, maintenance of the habitat
October 1999 – September 2001	**Employment** at the Energie-Aktien-Gesellschaft Mitteldeutschland (EAM), *Department Services* in Homberg: public relations, administration, customer service
June 1998 – September 1999	**Internships** in advertising agencies, course-related to the Akademie für Absatzwirtschaft Kassel: image editing, public relations, acquisition

International experience

April 2006 – July 2006	**Field trip** in the peruvian rainforest, project: population ecology of *Heliconia spp*., in collaboration with *Perú Verde* (Cusco) and the University of Marburg, working group of *Plant Ecology*

Scholarships, grants

August 2011 – März 2012	**Grant** of the advancement of women, University of Würzburg
April 2006 – July 2006	**Grant** of the Deutscher Akademischer Austauschdienst (DAAD) for facultative work experience in the peruvian forests

Teaching experience

Summer 2011	**Excursions** for bachelor students to different habitat types (introduction of trapping methods and identification of animals in the field)
December 2010	**Course** in Geographic Information Systems: Using the example of conducting a landscape mapping (first steps in ArcGIS)
May 2009 – January 2010	**Supervision** of bachelor students

Scientific qualifications

October 2011	**‚Linear Statistical Models with R‘** by C. Scherber and Y. Clough, Georg-August University, Göttingen
September 2010	**Biodiversity Exploratory Workshops** in Jena ‘Mixed Effects Models’ by J. Schuhmacher ‘Soft Skills’ by S. Pfeiffer
March 2010	**‘Introduction into ArcGIS’** by C. Baeßler, UFZ Halle
February 2010 – March 2010	**‘Generalised Linear Modelling’** by M. J. Crawley, Imperial College London

Methods

Statistics:

Generalised linear (mixed effects) models in R, correction of spatial autocorrelation (used packages: nlme, lme4, AED, MASS, MuMIn, lattice, spdep, gstat and others)

Phylogeny:

Maximum Parsimony, Maximum Likelihood, Bayesian Statistics, Alignments (using Modeltest, PAUP*, Mega, MrBayes)

Morphometry:

Elliptic Fourier Analysis

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