Scale dependence of pollinator community turnover and tritrophic interactions in changing landscapes

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M.Sc

Tatiane Beduschi

geboren in Blumenau, Brasilien

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1. Referent: Prof. Dr. Teja Tscharntke

2. Korreferent: Dr. Christoph Scherber

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"The fact is that no species has ever had such wholesale control over everything on earth, living or dead, as we now have. That lays upon us, whether we like it or not, an awesome responsibility. In our hands now lies not only our own future, but that of all other living creatures with whom we share the earth."

David Attenborough, *Life on Earth*

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SUMMARY

Agricultural landscapes account for approximately 40% of global terrestrial area and this proportion tends to grow due to the increasing demand for fuel, food and other agricultural products. For successful crop production in the future, it is crucial to preserve the ecosystem services performed by biodiversity in these areas. Understanding how land use and landscape composition affect species distribution and ecosystem functions is key to achieve this objective.

Organisms respond to habitat heterogeneity at different spatial scales, which needs to be considered in landscape studies. The temporal scale can also be meaningful, given that agricultural landscapes are highly dynamic environments and the frequent changes in land cover may affect ecological processes.

In this thesis we study local and landscape effects on plant-insect interactions, local diversity and community structure in changing landscapes. We focus on two landscape components that potentially influence insect communities and interactions: semi-natural habitats and oilseed rape fields (*Brassica napus* L.). Semi-natural habitats are stable environments that provide food and nesting resources constantly. Oilseed rape is a mass flowering crop that offers huge amounts of food resources in a short period of time.

We sampled landscapes using a grid design replicated in space and time. This multiscale approach allowed us to investigate:

(1) How different sampling designs can affect the estimate of biodiversity patterns.

(2) How the effect of landscape composition on a herbivore-parasitoid trophic interaction changes with time

(3) How landscape composition affects spatial community similarity at the landscape scale.

Chapter 1 introduces the topics covered in this thesis.

Chapter 2 shows how sampling whole landscapes can improve biodiversity estimates. Our aim was to determine how the predictability and stability of these estimates are affected by restricting sampling to only one habitat or to only few sampling points per area. We found that sampling organisms at a small spatial scale can influence the results of ecological studies when they use resources at large scales. Our results show that (i) the number of samples per study area affects the precision of parameter estimation and (ii) the selection of just one habitat type

for sampling may generate biased estimates of species richness. Moreover, we observed that the spatial scale of best predictions of the species richness of organisms, which is the landscape sector experienced by organisms, changes with the sampled habitat type. We conclude that estimates obtained by sampling limited to one habitat type or with few replicates per area will often not be representative of the landscape-wide population or community. Therefore, caution should be taken when generalizing too widely from such restricted studies.

In **Chapter 3,** we apply multi-level generalized path analysis to understand how the dynamics of agricultural landscapes affects the tritrophic interaction between pollen beetles (*Brassicogethes aeneus* F), their host plant oilseed rape and their parasitoids. We investigate how the effect of landscape composition (percentage of oilseed rape fields and non-crop areas) on herbivore and parasitoid abundance depends on the temporal scale of observation and whether system dynamics showed interannual carry-over effects. We found that the effect of oilseed rape fields on beetle abundance changed with time from negative to positive. Parasitism had a negative effect on the number of pollen beetles, but only in areas with a low proportion of oilseed rape. Interestingly, our path analysis revealed that landscape composition affected herbivore abundance one or two years later, mediated by changes in parasitism. These results indicate an interannual carry-over effect on plant-herbivore-parasitoid interactions, as the insects are affected by landscape composition and top-down effects in previous years.

In **Chapter 4,** we study the effect of landscape composition on spatial community turnover of pollinators. We compared solitary bee and hoverfly communities, both of which provide important pollination services, yet often show contrasting responses to landscape context. Our grid design allowed us to sample whole landscapes and provided insights on the exchange of individuals between habitats. While the proportion of oilseed rape did not explain spatial community turnover for either taxon, the flowering period influenced the effect of semi-natural habitats, which promoted the homogenization of bee communities during oilseed rape flowering and of hoverfly communities after flowering. The transience of the effect indicates that this pattern was caused by increased movement of individuals between habitats. This spatial homogenization of the community can be important to stabilize pollination in crop fields and to promote community resilience after disturbances, which is of socio-economic importance in agricultural landscapes.

In summary, the different habitat types that compose heterogeneous agricultural mosaic landscapes can play different roles for tritrophic interactions and the structure of insect communities. Larger proportions of semi-natural habitats may increase stability of pollination

and biological control by benefiting solitary bees, hoverflies and parasitoids. Mass flowering crops can influence insect communities and population densities, affecting ecosystem services both positively and negatively. This effect may be temporary, limited by the flowering period, or may extend to the following years, particularly for specialized insects, such as the pollen beetle and its parasitoids. This diversity of effects from different landscape components can be best investigated when all habitat types are sampled. Results originating from only one habitat type cannot be extrapolated to the whole landscape. In conclusion, landscape planning should take into consideration the movement of organisms between habitat types and through time in order to guarantee conservation of ecosystem services and crop yield.

CHAPTER 1

General Introduction

INTRODUCTION

Agricultural areas cover a large fraction of the Earth's surface and provide essential resources to human existence and quality of life (Tilman *et al.* 2002; Martin *et al.* 2012). However, recent agricultural practices that have greatly increased global food supply have had unintended, detrimental impacts on biodiversity and trophic interactions, affecting ecosystem services and highlighting the need for more sustainable methods (Sala *et al.* 2000; Tilman *et al.* 2002; Fahrig 2003). However, the development of such methods depends on the definition of the relevant temporal and spatial scales affecting organisms and their interactions.

Agricultural landscapes

Landscape-scale management holds great potential for increasing the sustainability of agriculture (Tilman *et al.* 2002), given that the distinct habitat types that constitute agricultural landscapes can affect biodiversity and ecosystem services differently. Nearby semi-natural areas can provide nesting and overwintering sites for insects that pollinate crops and contribute to efficient control of many pests (Thies *et al.* 2003; Ricketts *et al.* 2008; Garibaldi *et al.* 2011). Such areas offer spatiotemporal stability of resource availability, but at low concentrations (Gladbach *et al.* 2010; Tscharntke *et al.* 2012). In contrast, cropland areas are ephemeral as habitat structure lasts only one season and is destroyed during harvest and/or from soil manipulation (Wissinger 1997). Nevertheless, crop fields may provide temporary resources in much higher concentrations than semi-natural habitats, what can also be beneficial to functionally important insects (Westphal *et al.* 2003; Westphal *et al.* 2009). Especially mass flowering entomophilous crops, such as oilseed rape (*Brassica napus* L.), are valuable foraging habitats and positively affect the abundance of bumblebees (Westphal *et al.* 2003; Westphal *et al.* 2009), solitary bees (Le Féon *et al.* 2013) and hoverflies (Hänke *et al.* 2014). Oilseed rape is a highly subsidized biofuel crop and the increasing demand for the oil produced with its seeds has been followed by an increase in production (Fig 1) and in acreage (Alford 2003; Carré and Pouzet 2014) and a consequent growth of pest populations (Hokkanen 2000).

Sampling in agricultural landscapes

Even though agricultural landscapes account for 40% of the global terrestrial land use, only 12.5% of the ecological studies are performed in these areas (Foley *et al.* 2005; Martin *et al.* 2012). In contrast, although protected areas comprise only 13% of the Earth's surface, 63% of the studies are situated in these environments (Jenkins and Joppa 2009; Martin *et al.* 2012). Even when studies are carried out in agricultural landscapes, they focus on protected fragments

situated within these landscapes (Martin *et al.* 2012). This prevalence of studies performed in relatively pristine shows a bias for traditional ecological research away from human activity areas and indicates that ecologists still perceive humans as an exogenous, perturbing force (Collins *et al.* 2000; Fazey *et al.* 2005; Metzger *et al.* 2010). However, the productive agriculture areas have particularly high biodiversity potential

Fig 1. Production of rapeseeds (million t) in the European Union between 2003- 2009. Source: Eurostat

(Altieri 1999). The view of cropland as inhospitable matrix has not been confirmed and high species richness can often be found in this environment (Fahrig *et al.* 2011; Mendenhall *et al.* 2014). Nonetheless, the rapid growth of the human population puts increasing pressure on these environments, endangering communities in croplands. Therefore, it is crucial to recognize the importance of biodiversity in these areas and to understand how the hospitality of the world's agricultural lands can be maintained (Tscharntke *et al.* 2005; Fahrig *et al.* 2011; Mendenhall *et al.* 2014)

In this thesis a grid design was used with the objective of sampling all habitat types, including all available crop fields and semi-natural habitats. The uniform distribution of samples ensured that the number of samples coming from each habitat type was proportional to the area occupied by the habitat in the landscape. This design allowed the assessment of the importance of different habitat types for insects at landscape scale and their movement throughout the landscape. It was also possible to include different scales in each study.

Scale dependence

Given that agricultural landscapes are heterogeneous in space and time, both spatial and temporal scales can affect community structure and trophic interactions. In fact, virtually all ecological patterns and processes are sensitive to scale (Wiens 2002; Sandel *et al.* 2009). As space and time change, interactions between organisms and the environment change, often in complex ways (Wiens 2002). Different organisms perceive and respond to landscape structure at different scales (Wiens *et al.* 1993) and the scale of the observation defines which subset of ecological patterns, processes, and relationships we perceive.
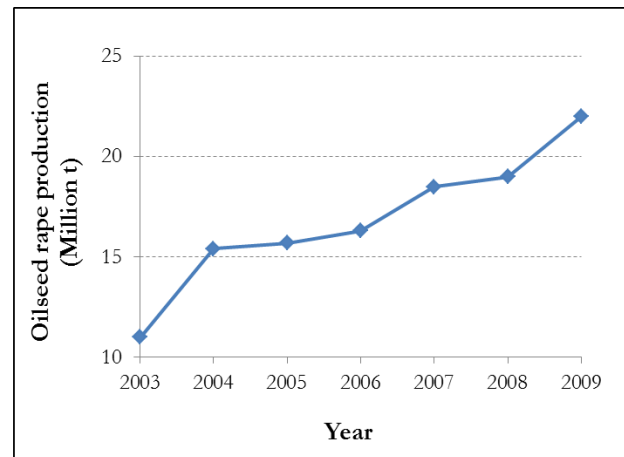
When resources are patchily distributed across space, an organism may consider a part of its habitat unsuitable, as the density of resource is too low, whereas in other parts resource availability is sufficiently high (Van de Koppel *et al.* 2006). Both the observational window of an organism and the area that it covers searching for resources are limited and will define the spatial range along which it will exploit the environment (Milne 1992; Van de Koppel *et al.* 2006). The spatial range is different for each species within a landscape and this, in turn, causes community structure to depend on a complex interplay between large- and local-scale processes (Menge and Olson 1990). This divergence in ranges can also influence the effect of landscape composition on trophic interactions, given that organisms at different trophic levels respond to environmental factors at different scales (Holt 1996; Van de Koppel *et al.* 2006). For example, while plants are affected by the microhabitat, herbivore populations are wider-ranging, but confined to the local community, and predators must be mobile enough to switch between patches of prey (Holt 1996). Consequently, the net interaction between two or more species may depend on the area over which it is measured (Sandel *et al.* 2009). In this sense, it is essential to include spatial scale explicitly in ecological studies in order to define at which scale ecological systems operate, i.e. which is the most efficient scale for management (Wiens *et al.* 2002).

While space has a crucial influence on ecological patterns, time also has a decisive role. In patchy environments, the temporal scale (i.e. patch duration) can even be a more important determinant of population size than the spatial scale (i.e. patch size) (Fahrig 1992). The relevant temporal scale affecting organisms and their interactions is also characteristic for each species (Fortin *et al.* 2002) and can be dependent on the life-cycle, longevity (Robertson and Kaufmann 1998) or metabolism rate (Fortin *et al.* 2002). Therefore, considering a larger time period can affect our assessment of community composition as a species which is dominant at one point in time may become unimportant at the next (Kremen *et al.* 2002; Gagic *et al.* 2012). Trophic interactions have also been shown to vary with time due to changes in community structure (Bell *et al.* 2002; Gagic *et al.* 2012) or in the surrounding environment (Thies *et al.* 2008).

Pollinator richness and community similarity

Wild plants and crops are highly dependent on pollination provided by wild animals (Kearns *et al.* 1998; Klein *et al.* 2007), given that managed honey bees cannot replace the contributions of diverse native insect communities for a wide variety of plants (Kremen *et al.* 2002; Garibaldi *et al.* 2013). In fact, richness of pollinator species has been shown to increase both visitation rates by wild insects and fruit set, independent of honey bee visitation (Garibaldi

et al. 2013). It is therefore of critical importance to understand the determinants of pollinator richness throughout the landscape in order to maintain viable pollinator communities in farmlands (Öckinger and Smith 2007).

Most studies focus almost exclusively on the effect of landscape context on pollinator species richness, rather than on community composition, which can change substantially, often resulting in a decline of more sensible species (Laurance *et al.* 2000; Carré *et al.* 2009; Tscharntke *et al.* 2012). Even with the reduction in area of high-quality habitats, landscape-wide species richness can remain constant due to increased beta-diversity among patches (Tscharntke *et al.* 2002). Nonetheless, this numerical compensation might conceal changes in community composition and the prevalence of common taxa (Carré *et al.* 2009). In this sense, community similarity can be a more appropriate diversity measure, given that it can better assess changes in community composition (Dormann *et al.* 2007).

Landscape composition can be expected to influence community similarity, as alterations in the size, connectivity and shape of high quality habitats can cause losses of specialist and rare species or disrupt the exchange of organisms between local communities, reducing spatial similarity (Tscharntke and Brandl 2004; Vandvik and Birks 2004; Dormann *et al.* 2007). The exchange of pollinators between habitat types has important consequences both for plants and for the pollinators themselves. For insects that nest in semi-natural habitats, the access to resources available in the cropland, such as those offered by mass flowering crops, may have positive effects on population size (Westphal *et al.* 2003; Westphal *et al.* 2009). For plants, higher pollinator species richness can increase visitation rates and guarantee stability of pollination services (Garibaldi *et al* 2011). Thus, increasing the movement of pollinators towards cropland can positively affect yield of animal pollinated crops, which account for 35% of the global food production and contribute vital micronutrients and dietary variety (Klein *et al.* 2007; Eilers *et al.* 2011; Vanbergen 2013).

Ecosystem services and trophic interactions

Biological control of pests in arable fields is an important ecosystem service (Thies *et al.* 2011) as most potential pests are not controlled by pesticides but natural enemies (Schmidt *et al.* 2003; Tscharntke *et al.* 2005). Parasitoids are one of the key agents for biological control (Schmidt *et al.* 2003; Thies *et al.* 2005; Gagic *et al.* 2012), and jointly with their hosts and associated host plants, comprehend over half of all known species of multicellular organisms (Hawkins 2005). Therefore, understanding how landscape composition can affect host-

parasitoid abundance is of crucial importance to preserve ecosystem services and stability in the future.

As a model system, I studied the tritrophic interaction involving the pollen beetles (*Brassicogethes aeneus* F.), their host plant oilseed rape, and their parasitoids (*Tersilochus heterocerus* Thomson; *Phradis interstitialis* Thomson and *P. morionellus* Holmgr.). The pollen beetle was chosen as focal organism because this is one of the numerically most abundant insect herbivores in Central Germany (Ryszkowski *et al.* 2001). The pollen beetles feed on pollen from a variety of flowers, but are dependent on crucifers (Brassicaceae), such as the oilseed rape, for reproduction. The parasitoids feed on nectar and are also highly specialized, laying eggs exclusively on pollen beetle larvae (Nilsson 2003; Gladbach *et al.* 2010). Pollen beetles and parasitoids have an univoltine life-cycle (Box 1), what indicates that the population emerging in spring was born in the previous year.

It has been shown that landscape composition affects pollen beetle abundance (Valantin-Morison *et al.* 2007; Zaller *et al.* 2008a; Rusch *et al.* 2013) and parasitism rates (Thies and Tscharntke 1999; Thies *et al.* 2003; Gladbach *et al.* 2010; Rusch *et al.* 2011), mainly at large scales. However, even though both spatial and temporal scales are important to understand trophic interactions and population dynamics (Kareiva 1990; Fahrig 1992; Pickett and Cadenasso 1995; Roland and Taylor 1997; Thies *et al.* 2005), most studies have focused only on the effect of spatial scale and one habitat type.

BOX 1. Life-cycle of pollen beetles and parasitoids

The details of the life cycles of beetles and parasitoids according to the season are presented (Fig B1).

Pollen beetles

The pollen beetle (*Brassicogethes aeneus F.*) emerges in early spring, after overwintering in the soil of field margins or woodlands, and feeds on pollen of various species of plants before migrating into oilseed rape fields (Nilsson 1988; Williams 2010). They arrive in the fields during bud stage and will feed on pollen by chewing into the buds, where they will also oviposit (Nilsson 1988; Ekbom and Borg 1996). The larvae feed on pollen and will eventually drop to the soil to pupate. The development from egg to adult takes about one month (Williams 2010). The newly emerged
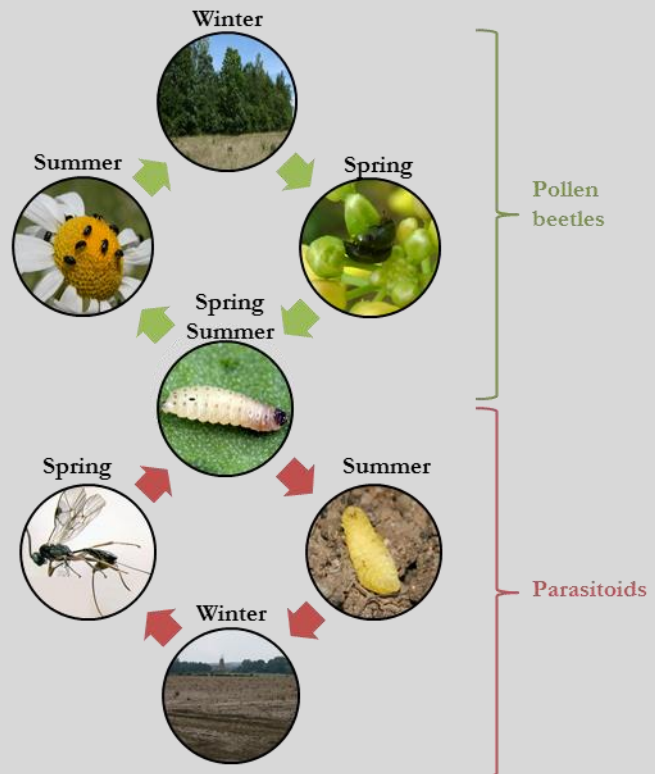

Fig B1. Life cycles of the pollen beetles and univoltine parasitoids. Photos by Christoph Scherber, Christoph Rothenwöhrer , Tatiane Beduschi and from Wikimedia Commons licensed under Creative Commons

pollen beetles will feed on the pollen of different flowers, since the flowering of oilseed rape fields will have ended (Hokkanen 2000). Adults of the first generation die after egg laying and, in late summer, the new generation of beetles seeks overwintering sites and will only reproduce in the following year (Nilsson 1988; Williams 2010).). The main damage caused by pollen beetles happens during the bud stage, since feeding and oviposition cause bud abscission, what can reduce yield (Zaller *et al.* 2008b; Williams 2010).

Parasitoids

During the larval stage, pollen beetles might be attacked by specialized parasitoids. The three most common species are *Tersilochus heterocerus* (Thomson), *Phradis interstitialis* (Thomson) and *Phradis morionellus* (Holmgren). The parasitoid egg is laid inside the pollen beetle larvae and will hatch once these drop to the soil to pupate. In the soil, the parasitoid larva completes its feeding and pupates. Parasitoids overwinter as diapausing adults in the soil of the oilseed rape fields and emerge in the following spring (Jourdheuil 1960; Nilsson 2003).

METHODS

The research was conducted in 10 landscapes (Fig 2) in the surroundings of Göttingen (51° 32' N, 9° 56' E) in Central Germany. The region is dominated by intensive agriculture interspersed with semi-natural non-crop areas like meadows, calcareous grasslands and woodlands (Steffan-Dewenter *et al.* 2002). The sampling landscapes were approximately 1km x 1km wide (mean area± SD= 0.93± 0.23km^2) and represented gradients of percent area occupied by oilseed rape fields and semi-natural habitats. Semi-natural areas were extensively managed areas including forest margins, calcareous grasslands, pastures and meadows. In each landscape, sampling was performed following a 5x5 grid. The grid was laid out over the landscapes in such a way to always include forest margins and grasslands as well as crop fields, while excluding cities or villages.
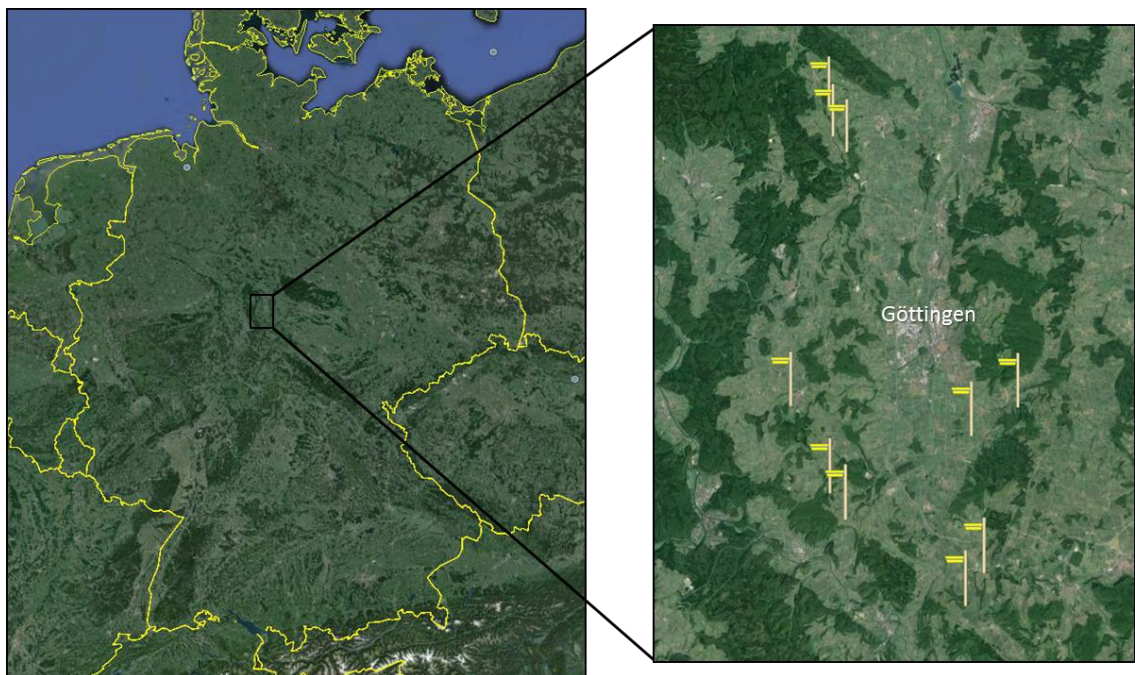
Fig 2. Locations of the ten sampling landscapes in the surroundings of Göttingen in Central Germany. Images from Google Earth

At each of these 25 points per landscape, yellow pan traps filled with salt water and a drop of detergent were placed. The traps were made of 500 ml plastic bowls with the inside sprayed with an UV-reflecting paint. Traps were placed at vegetation height (Fig 3a) and exposed for three days in each of four periods: May 2011 and 2012 (during oilseed rape flowering- Fig 3b) and June 2011 and 2012 (after oilseed rape flowering- Fig 3c). Considering that 30 pan traps were damaged, there was a total of 970 samples. All samples from the pan

traps were sorted, pollen beetles were counted (Fig 4) and bees and hoverflies were separated and sent to specialists for identification.
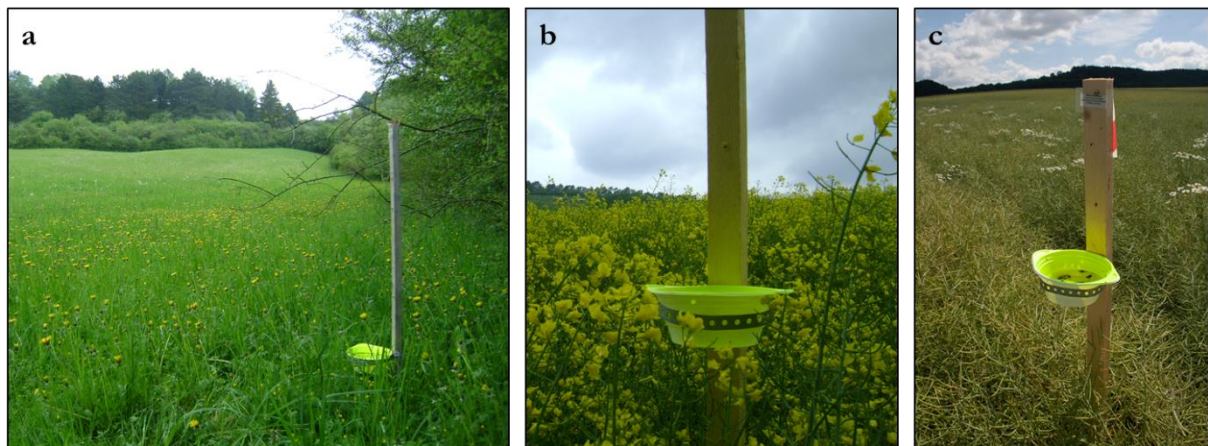

Fig 3. Examples of pan traps placed (a) at semi-natural habitats, (b) at oilseed rape fields during flowering (c) and after flowering. Photos by Christoph Scherber and Tatiane Beduschi.

Additionally, in May 2011 (at peak oilseed rape flowering), the flowers of five oilseed rape plants were collected in each grid point located in an oilseed rape field (N= 58). Wild flowers in non-crop areas were also inspected, but no pollen beetle larva was found outside oilseed rape flowers. All larvae located within the sampled flowers were counted and, in each sample, 20 individuals were dissected in order to determine the parasitism rate. In the grid points where no larvae were present, the parasitism rate was defined as zero.

Satellite-based image classification was used to measure proportions of oilseed rape fields and non-crop areas, which include meadows, pastures and forests. Percentage of non-crop area has been shown to be a robust criterion for the quantification of habitat complexity as it tends to be closely correlated with other landscape metrics such as habitat diversity (Thies and Tscharntke 1999). These measurements were done for the years of 2010, 2011 and 2012 and for all study areas.

Fig 4. Sorting of insects and counting of pollen beetles Photo by Tatiane Beduschi

While proportion of oilseed rape fields changed greatly through time, due to crop rotation, proportion of non-crop area did not change in the studied years. Satellite imagery was provided by RapidEye™ and image classification was performed using ENVI EX® and ESRI® ArcMap™10.

RESEARCH OBJECTIVES

In this thesis I study local and landscape effects on plant-insect interactions, local diversity and community structure in changing landscapes. The aim was to answer the following questions:

(1)   How do different sampling designs can affect the estimate of biodiversity patterns?

(2)   How does the effect of landscape composition on a herbivore-parasitoid trophic interaction change with time?

(3)   How does landscape composition affect spatial community similarity of pollinators at the landscape scale?

CHAPTER OUTLINE

Chapter 2 focuses on the first question. More specifically, it assesses: (i) how the number of sample points per area affects the outcome of models; (ii) how the number of sampled habitats and habitat types influences the model estimates; (iii) how the scale (i.e. radius of landscape sector) best predicting bee diversity is affected by sampling habitat. To achieve this goal, a subset of bee samples collected only in one habitat type (semi-natural habitats or oilseed rape fields) was compared with samples of different sizes placed systematically in the landscape, comprising a variety of habitat types.

Chapter 3 addresses the second question using as a model system the interaction between pollen beetles, their host plant (oilseed rape) and their parasitoids. I investigated: (i) if the parasitism rate is more strongly affected by host plant abundance (proportion of oilseed rape) in the previous or in the current year; (ii) whether the effect of different landscape components on herbivore abundance changes over time; (iii) if beetle abundance is driven by carry-over effects that span multiple years. To study these complex relationships through time a multilevel generalized path analysis was applied.

Chapter 4 focuses on the third question. I compared solitary bees and hoverflies, which show contrasting responses to landscape structure due to distinct resource requirements and dispersal abilities (i.e. foraging ranges). The following hypotheses were tested: (i) spatial community turnover within landscapes is affected by landscape context, i.e. proportion of semi-natural habitats and/or of oilseed rape fields, due to altered species exchange between local communities; (ii) hoverfly communities are generally more homogeneously distributed throughout the landscape and are, therefore, less affected by landscape context than solitary

bees; (iii) spatial community turnover is driven by the proportion of oilseed rape flowering, which is most influential during the flowering period. Semi-natural habitats and other crop fields have a more relevant role for bees and hoverflies after blooming.

Chapter 5 offers a summary of the results obtained in each study and conclusions emerging from all of them taken together.

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CHAPTER 2

Improving biodiversity estimates through sampling landscapes across habitat types

Tatiane Beduschi, Teja Tscharntke and Christoph Scherber

ABSTRACT

An appropriate sampling design for biodiversity estimates holds crucial importance in ecological studies, given that sampling biases can yield incorrect estimates and lead to erroneous inferences. Although most species use resources at larger spatial scales and across habitat types, thereby linking habitats on a landscape scale, ecological studies tend to be performed only in one type of habitat. This may result in biased biodiversity estimates due to a non-probabilistic design, with potential sampling units having a null or unknown chance of being selected. Our aim was to determine how restricting sampling to only one habitat type, number of sampling points per area and spatial scale considered affect the predictability and stability of biodiversity estimates.

In this study, we focused on bee species richness in agricultural landscapes and analyzed how consideration of (i) all managed and semi-natural habitat types and (ii) landscape composition at different spatial scales contributes to reliable estimates. We compared bee richness predictions based on samples collected only in one habitat type (semi-natural habitats or oilseed rape fields) with samples placed systematically throughout the landscape, covering all available habitat types. Fifty variations of each subset were created to obtain a wide range of possible estimates.

Our results show that limiting the sampling to one habitat type led to biased estimates of the landscape-wide bee species richness, even when the number of samples was increased in this habitat. The spatial scale of best predictions, i.e. the landscape sector experienced by the bees, was also dependent on sampling habitat. Species richness was overestimated when sampling was limited to semi-natural habitats and underestimated in oilseed rape fields. In addition, sample size was influential, with estimate precision improving when number of samples increased.

In conclusion, sampling organisms at a small spatial scale when they use resources at large scales can negatively affect the results of ecological studies. First, the spatial scale to be considered depends on the landscape-wide resource use, which is species or group specific. Second, limiting the sampling to one habitat type can lead to wrong decisions about the value of the target habitat for conservation, resulting in spurious projections or unreliable species distribution models. Third, increasing the number of sampling units improved precision. We suggest that biodiversity studies increase the range of sampling area to the landscape level to include all habitats that provide potential resources.

INTRODUCTION

Sampling procedures can affect results of community and population ecology studies (Kenkel *et al.* 1990). Sampling biases can, for example, reveal incorrect patterns of species distribution and community structure (Kodric-Brown and Brown 1993). Studies aiming to relate local and landscape contexts to population and community processes face particular sampling challenges due to the difficulties in scaling up from small to large scales (Scherber *et al.* 2012). Frequently used approaches consist of sampling only one or a few locations within a landscape and relating it to local or landscape contexts (e.g. Steffan-Dewenter *et al.* 2002; Chust *et al.* 2003; Tscharntke *et al.* 2005; Concepción *et al.* 2008; Tscharntke *et al.* 2012). However, this method can prove inadequate if it aims to extrapolate the sampling results from one point or habitat to the whole landscape, not considering the spatial heterogeneity inherent within the landscape (Edmunds and Bruno 1996). This aspect holds great importance, especially considering that many parts of the world are now a patchwork of land uses and ecosystems extending from "natural" to "intensively managed" gradients (Hobbs *et al.* 2006). Even though natural protected areas are important in terms of preserving biodiversity, the landscape beyond their boundaries also have ecological value, providing resources and migration routes for many populations of endangered species (Willis *et al.* 2012)

In spite of this ecological potential of non-protected areas, ecological studies tend to be situated in sites under some form of legal protection, despite such areas representing less than 15% of Earth's ice-free land (Jenkins and Joppa 2009; Martin *et al.* 2012). Additionally, only 12.5% of study sites have been described as agricultural/rangeland, whereas these kind of habitats account for 40% of global terrestrial area (Martin *et al.* 2012).

This kind of selective sampling can cause a number of problems. In a non-probabilistic sampling design, within which some sampling units within the sampling frame have unknown or no chance of being selected, the resulting estimates can be biased and might produce erroneous inferences (Lemeshow and Levy 1999; Yoccoz *et al.* 2001). In order to ensure reliability, a sampling design should yield parameter estimates that are both unbiased (i.e. mean value of estimates equal to the target population value) and precise (i.e. small variability) (Lemeshow and Levy 1999). In a probabilistic design, whereby all sampling units have a known or equal chance of being selected, it is possible to obtain unbiased estimates of the mean and variance (Lemeshow and Levy 1999). Therefore, if the population or community of interest does not exclusively occur in protected or natural areas, but also disperses into the matrix (e.g. Law *et al.* 1999; Brotons *et al.* 2003; Haynes *et al.* 2007), sampling units should be located in all habitat types within the landscape, given that the scale of the sampling frame should coincide

with the distribution pattern of the target population (Särndal *et al.* 1992). This is particularly true for highly fragmented areas where the matrix also offers resources, as is the case in agricultural landscapes (Dunning *et al.* 1992; Norton *et al.* 2000).

Accordingly, a large body of literature recommends sampling procedures including larger scales, in order to encompass a wider range of spatial heterogeneity (e.g. Levin 1992; Norton *et al.* 2000; Whittaker *et al.* 2001; Yoccoz *et al.* 2001). This would allow a more complete assessment of spatial and temporal variation in the biological responses to environmental factors. Additionally, it would help to avoid truncated gradients that occur when part of the range of the biological or of the environmental variable is not included in the sampling frame (Albert *et al.* 2010). This is important given that truncated gradients can lead to inaccurate statistical inference and, consequently, to false ecological interpretation (Thuiller *et al.* 2004).

Despite the importance of sampling design being widely recognized, no published studies reveal how the selection of the sampling habitat combined with the number of sampling points per area of interest can affect the stability of results of ecological studies. Traditionally, researchers will choose one location or habitat in a landscape to sample, in a method hereafter termed as the "habitat-selection method". As an alternative, we suggest a design where samples are placed randomly or regularly throughout the landscape. This way, habitats will be sampled in a similar proportion to the area that they occupy in the landscape. This sampling method will be henceforth called the "landscape-grid method", since in this paper we used a regular sampling approach. Our aim is to investigate how these sampling aspects can influence the conclusions reached by ecologists. We use a comprehensive dataset collected in 10 replicated landscapes, with each comprising 25 sampling points, to test the following hypotheses:

(1) the number of sample points per area will affect the outcome of models

(2) the diversity of sampled habitat types will influence the model estimates

(3) the scale (i.e. radius of landscape sector) best predicting bee diversity will be affected by sampling habitat

More specifically, we compare a subset of bee samples collected only in one habitat type (semi-natural habitats or oilseed rape fields) with samples of different sizes placed systematically in the landscape, comprising a variety of habitat types. Finally, we discuss the implications of using a reduced sampling design. Proportion of oilseed rape was chosen as a determinant of bee species richness, given that this landscape feature is known to have the strongest effect on bee diversity (e.g. Diekötter *et al.* 2010; Holzschuh *et al.* 2011; Westphal *et al.* 2003), while proportion of semi-natural habitats is not a limiting factor (Westphal *et al.* 2003).

METHODS

Data compilation

The study was performed in 10 landscapes in the surroundings of Göttingen (51° 32' N, 9° 56' E) in Central Germany in 2011. The landscapes were approximately 1km x 1km wide (mean area± SD= 0.93± 0.23km^2) and represented gradients of percent area occupied by oilseed rape fields and semi-natural habitats, which were not correlated. Sampling was performed in a 5x5 grid, which was laid out over the landscapes in such a way to always include forest margins and grasslands (semi-natural habitats) as well as crop fields, while excluding cities or villages.

Yellow pan traps filled with water were placed in each cell of the grid and exposed for three days in June 2011 (after oilseed rape flowering), because the highest bee abundance and species richness can be observed during this month (Holzschuh *et al.* 2011).

As three pan traps were damaged, we had 247 samples overall. All wild bees were sent to specialists for identification. Sampling habitats included oilseed rape fields, cereal fields and semi-natural habitats, which comprised grasslands and forest margins Satellite-based image classification was used to measure the proportion of oilseed rape at six different scales. These scales were represented by 6 nested circles with the following radii: 0- 100m, 100- 250m, 250- 500m, 500- 750m, 750- 1000m and 1000- 1500m, using ESRI® ArcMap™10. Satellite imagery was provided by RapidEye™.

Data resampling

In order to compare the landscape-grid method with the habitat-selection method, we took two subsets of our data that included samples collected only in semi-natural habitats (five points per landscape; total= 50) or only in oilseed rape fields (mean points per landscape± SD= 6.2± 5.65; total= 56). These habitats were chosen as they represent two extremes. The semi-natural habitats are protected areas and tend to be preferred for ecological studies. The oilseed rape fields represent very homogeneous agricultural areas. In each landscape, one point within the chosen habitat was sampled, creating a new dataset (N= 10) that was subsequently analyzed (see section Statistical Analyses). This procedure was repeated 50 times per subset (semi-natural habitats and oilseed rape fields) to obtain a wide range of possible results, resulting in two sets of model results, one for semi-natural habitats and one for oilseed rape fields, each containing 50 outcomes.

To determine how the number of samples per landscape affects the results, we randomly sampled 5, 10, 15 and 20 points per landscape from the full dataset (N= 247), with each of the new datasets subsequently analyzed (N= 50, 100, 150 and 200, respectively). This was also repeated 50 times for each subset of number of points, resulting in four sets of model results each with 50 outcomes.

Overall, we created the following three datasets that were used for statistical analysis:

(1) all data points collected only in semi-natural habitats;

(2) all data points collected only in oilseed rape fields; and

(3) all data points collected following a regular grid approach.

A summary of the resampling methods can be seen in Table 1. The selection of points for the new datasets was always repeated 50 times, with each of these new datasets analyzed accordingly. The complete datasets were also analyzed to detect the effect of sampling only one kind of habitat several times per landscape. Moreover, these full datasets were also used to create species accumulation curves for each of the datasets, with the objective of determining how sampling affects estimates of species richness.

Table 1. Summary of sampling habitat and number of sampling points considered for resampling and analyses. New dataset refers to the six groups of 50 datasets created by resampling. Complete dataset indicates all points sampled within the mentioned habitat(s). Sampling area indicates each one of the 10 landscapes where sampling was performed.

Sampling habitat	Number of sampling points in the new datasets (per sampling area)	Number of sampling points in the complete datasets
All habitats	5, 10, 15 or 20	247
Oilseed rape fields	1	56
Semi-natural habitats	1	50

Statistical Analyses

We determined the relevant spatial scale(s) using linear models fit by generalized least squares (GLS) as these models allow the explicit incorporation of spatial autocorrelation by fitting a variance-covariance matrix (Dormann *et al.* 2007). This model type also allowed us to perform automatic model simplification, which would not be possible with other models that also account for spatial autocorrelation. The response variable was bee species richness. This variable was log transformed (*ln (y+1)*) as the response variable was log-normally distributed. The initial explanatory variables were the proportions of the area occupied by oilseed rape within the six aforementioned scales.

All models were simplified by stepwise deletion of terms from maximal models until Akaike's Information Criterion (AIC) reached a minimum. According to this method, all parameters remaining after model simplification had relevant explanatory power (Crawley 2013). When more than one point per landscape was sampled, we defined a spherical correlation structure using the coordinates of the sampling points and the landscapes as a grouping variable to account for spatial autocorrelation. To avoid differences emerging from variable statistical methods, we applied GLS models even when only one point per landscape was considered. All analyses were performed using R 2.15.1 (R Core Team 2012). GLS models were implemented using the function gls from the "nlme" package 3.1-104 (Pinheiro *et al.* 2012). Stepwise model simplification was performed using the stepAIC function from the "MASS" package (Venables and Ripley 2002), corrected for small sample sizes (i.e. employing AICc rather than AIC; Burnham and Anderson 2002).

The species accumulation curves were constructed using the specaccum function from the "vegan" package 2.0-7 (Oksanen *et al.* 2013). Sites were added at random, with 500 permutations performed.

RESULTS

Overall, we collected 76 bee species, excluding *Apis mellifera* (Linnaeus, 1758). Thirty per cent of the species (n=23) were not found in semi-natural habitats and 55% (n=42) were not found in oilseed rape fields. There was also great variability observed among sampled points within each landscape (Fig 1). When only one point per landscape was sampled, often no scale (i.e. radius of landscape sector) was selected as relevant (72% of the times for semi-natural habitats and 56% for oilseed rape fields; Fig 2a) or found to be significant (80% and 60% of the times for semi-natural habitats oilseed rape fields, respectively; Fig 2b). Additionally, no clear pattern identifying a preferred radius was recognized. However, with an increasing number of points sampled in a landscape, it was possible to detect a growing precision, with the 750-1000m scale chosen as relevant and significant in the majority of the models (Fig 2a and b). When 20 points per landscape were sampled, this scale was statistically significant in 94% of the 50 models performed (Fig 2b).
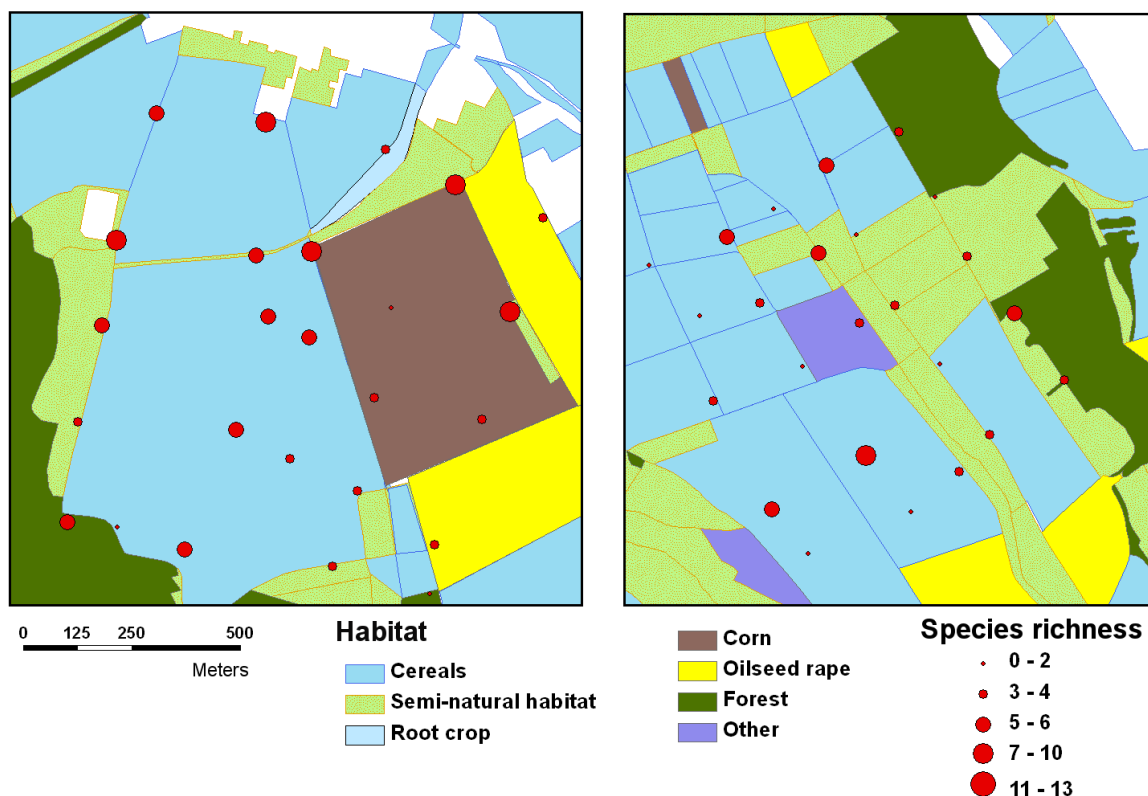
Fig 1. Examples of grid-based sampling showing pollinator richness in study areas. Circles represent the location of samples and size of circles is proportional to the number of species found in each sampling point. Figures show the landscape around the villages of Hohengandern (UTM coordinates- 32U 565842.636mE, 5690886.797mN) and Espol (32U 555000.087mE, 5728428.317mN).
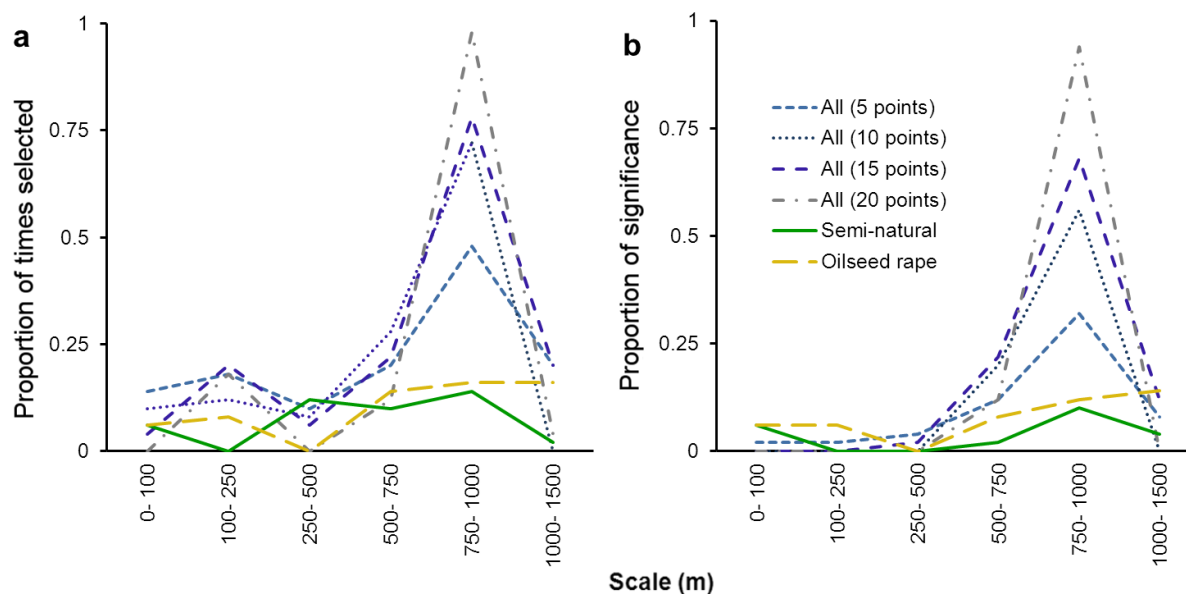

Fig 2. Summary of the outcomes of the generalized least square models. (a) Proportion of times a scale was kept in the model after stepwise selection. (b) Proportion of significant results for each scale ($p < 0.05$). "All" represents sampling throughout the landscape. "Semi-natural" and "Oilseed rape" represent one point sampled in each of the mentioned habitats.

When the whole ensemble of points collected in oilseed rape fields was analyzed in a single model, only the 1000-1500m radius remained in the final model after stepwise selection (Table 2). This means that this is the only scale that can explain the data. The model performed using the semi-natural full dataset selected the same scale as the model that included all 247 systematically sampled points (750-1000m). Nonetheless, the estimate from this full semi-natural habitat model was very different from the one resulting from the landscape-grid method (Table 2; Fig. 3). In the semi-natural habitat model, none of the points sampled presented a proportion of oilseed rape greater than 0.3 and only a few exceeded 0.2. This constitutes a truncated oilseed rape gradient, which means that part of the range of the environmental variable was not included in the sampling frame (Albert *et al.* 2010). As a result, the expected number of bee species in the missing range was clearly underestimated in the outcome of the model, when compared to the landscape-grid method.

Table 2. Scales kept in the model by stepwise selection, parameter estimates, standard error of the mean of three generalised least squares models performed on the complete datasets of points collected in semi-natural habitats, oilseed rape fields and following a grid throughout the landscape. Asterisks represent significant results ($p < 0.05$).

Sampling habitat	Relevant scale	Estimates	SEM	N
All habitats	750- 1000m	-1.72*	0.46	247
Oilseed rape fields	1000- 1500m	-2.31*	0.93	56
Semi-natural habitats	750- 1000m	-4.07*	1.55	50

The estimates of bee richness in relation to percentage of oilseed rape fields, when considering only one point per landscape, were very variable, independent of the sampling habitat selected, and fluctuated from negative to positive values (Fig 4). Furthermore, we found a gradual increase in the precision of the estimates and reduction in bias with a growing number of points included in the sampling, as a larger proportion of the models approached the estimate of the complete model including all 247 points sampled (Fig 4).

Additionally, the species accumulation curves showed that sampling preferentially in one habitat type can result in different estimates of species richness, depending on the chosen environment (Fig 5). If only semi-natural habitats were sampled, more species were collected per sample in comparison to the landscape-grid method. On the other hand, when samples were collected only in oilseed rape fields, the curve grew less steeply.
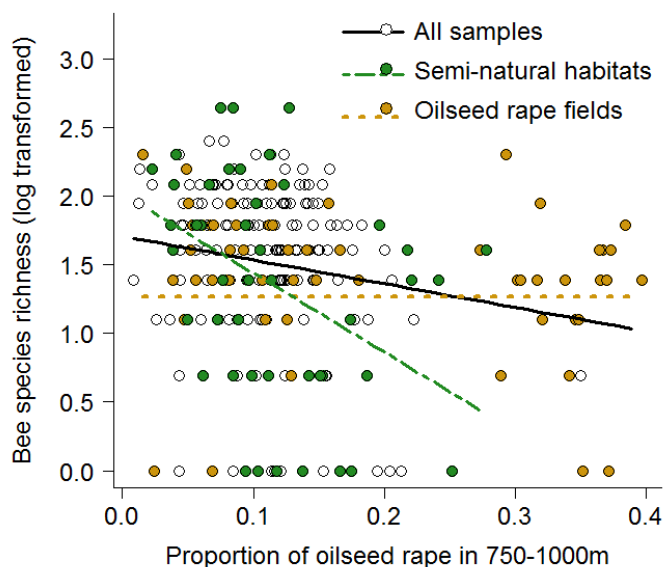
Fig 3. Relationships between bee species richness (log transformed) and proportion of area occupied by oilseed rape within a buffer area ranging from 750 to 1000m distance from the sampling point. Data points constituting the full dataset are generally represented by black circles. Yellow and green filled circles represent samples from oilseed rape fields and semi-natural habitats, respectively. Lines represent the predicted estimates from the generalized least squares models.

DISCUSSION

Our study shows that number of samples per area and sampling habitat affect the estimation of the landscape–wide bee species richness. First, we found that limiting sampling to only one point per landscape can be problematic, given that individual points are subject to local stochasticity. Estimates depended on the sampling points chosen, as a consequence of the great variation found among possible sampling points in the landscape. Moreover, all of the considered radii had equal chances of explaining the data (Fig 3), thus reinforcing the great variability of possible outcomes when only one point per landscape is sampled. This unaccounted randomness could reflect the cause of the lack of consensus in some issues in ecology. For example, several studies have focused on the effect of proportion of oilseed rape fields in the landscape on pollen beetles *Brassicogethes aeneus* (Fabricius, 1775), a pest of oilseed rape, reaching very different conclusions. Rusch *et al.* (2011) did not find an effect, while Valantin-Morison, Meynard and Dore (2007) observed a positive correlation and Zaller *et al.* (2008) found a negative correlation between proportion of oilseed rape and pollen beetle abundance.
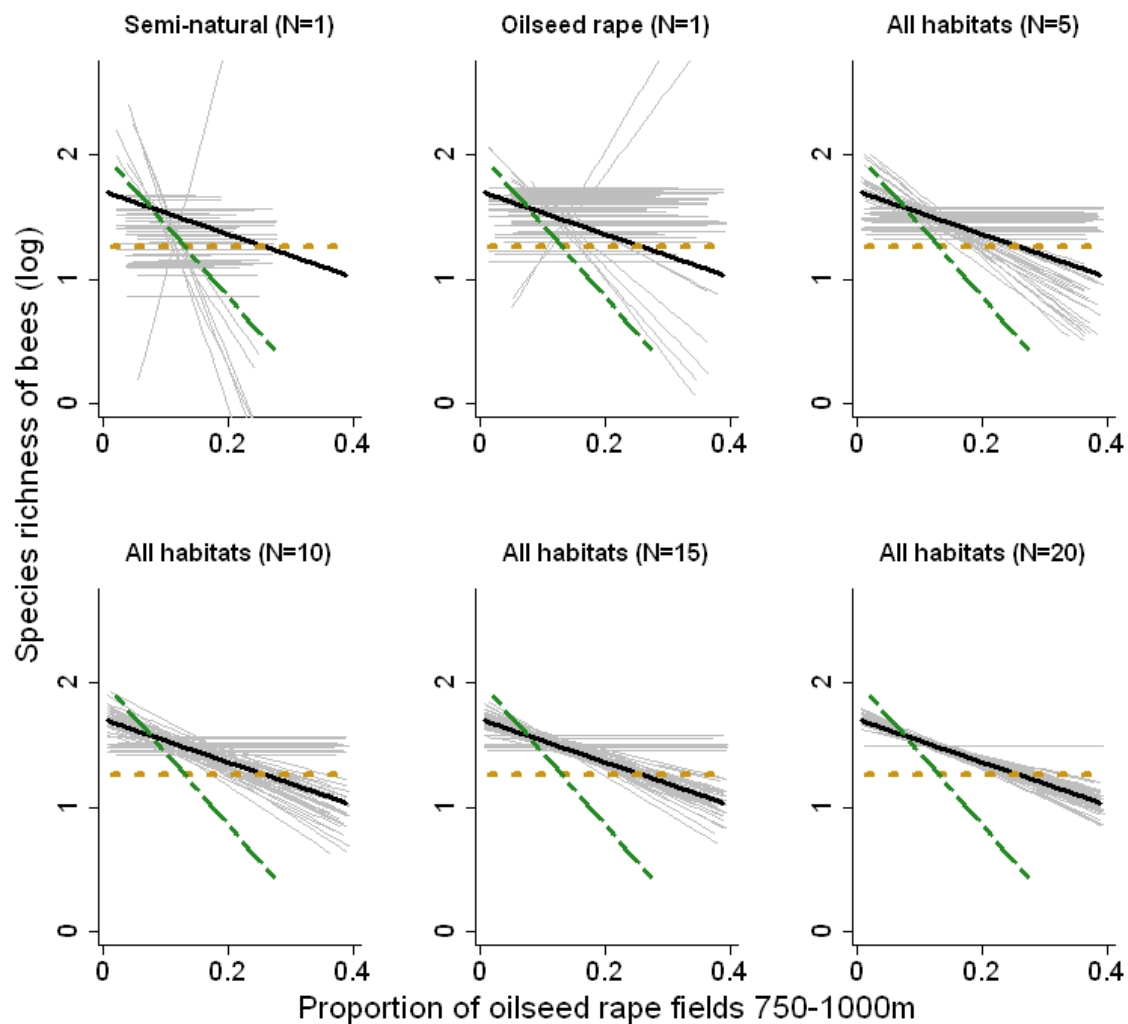
Fig 4. Relationships between bee species richness (log transformed) and proportion of area occupied by oilseed rape within a buffer area ranging from 750 to 1000m distance from the sampling point. Yellow, green and blue lines show the predictions made by generalized least squares models for all the data points collected in oilseed rape fields, semi-natural habitats and following a grid throughout the landscape, respectively, as seen on Fig 3. Each grey line represents the outcome of a generalized least squares model performed in each of 50 datasets created according to the following rules: 1 point per area sampled in semi-natural habitats (top left); 1 point per area sampled in oilseed rape fields (top centre); 5 random points per landscape (top right); 10 random points per landscape (bottom left); 15 random points per landscape (bottom centre) and 20 random points per landscape (bottom right).
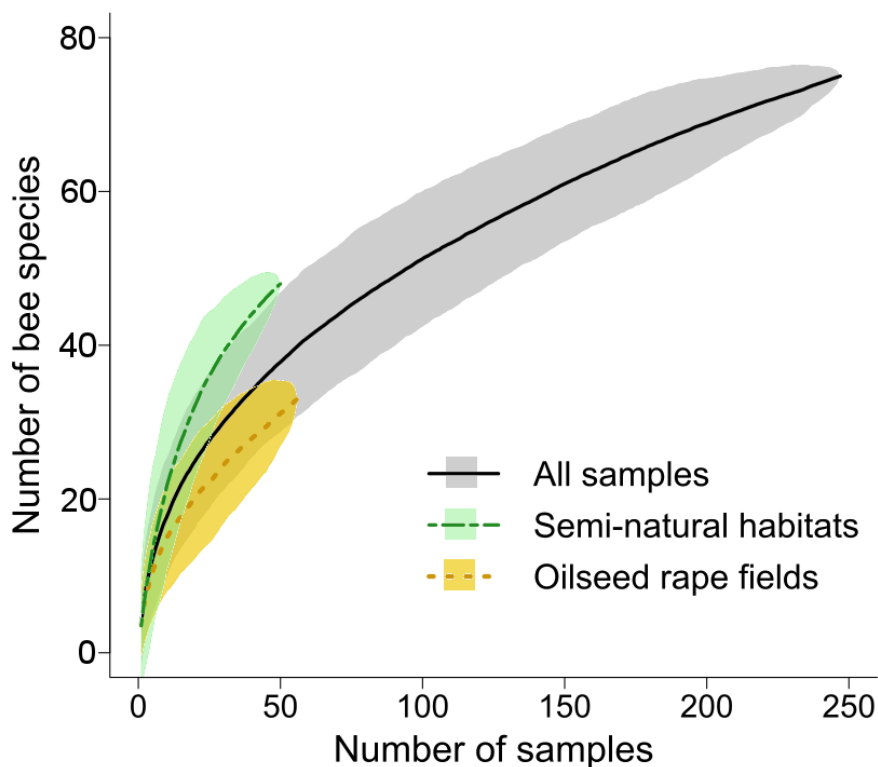
Fig 5. Smoothed average bee species accumulation curve produced by 500 random reorderings. Buffer around lines represent confidence intervals. Yellow, green and red lines represent data collected in oilseed rape fields, semi-natural habitats and using systematic sampling, respectively.

Our results show that limiting the sampling to one habitat type can lead to biased estimates which cannot be extrapolated to the whole landscape. This was observed even when the number of samples in that habitat was increased. This can happen, as was the case with the semi-natural habitat samples, because ecological studies often do not encompass the full range of possible environmental conditions. These incomplete gradients cause misestimations to occur, generating unpredictable effects on the species' response curves, independent of the data distribution (Mohler 1983). Additionally, using data collected in one habitat to predict species richness at the landscape scale might yield spurious projections or unreliable species distribution models. This would result from the inaccurate estimated curves, given that they are incomplete descriptions of the responses of species to environmental predictors (Thuiller *et al.* 2004). Edwards *et al.* (2006) compared how predictions based on a probabilistic vs. a non-probabilistic sampling design reflect the real pattern of lichen species distribution, and found that a systematic grid sampling produces more realistic results than a purposive, non-random sampling strategy.

Moreover, an incomplete sampling, that does not capture the whole community, can also lead to incorrect decisions about conservation. For example, Kodric-Brown and Brown

(1993) repeated a study by Glover (1989) on fish species in Australian desert springs, correcting known biases due to incomplete sampling in the first study. The subsequent study showed that the conservation goals established by the paper by Glover (1989) were incorrect as the species initially identified as the most endangered was actually common and, therefore, protection efforts should focus on two other species that proved to be the least frequent.

Another important result of our study is that the species accumulation curve was overestimated when sampling was restricted to semi-natural habitats and underestimated when focused only on oilseed rape fields. Comparable results have been found in vegetation studies (Diekmann, Kühne and Isermann 2007; Michalcova *et al.* 2011), when preferential sampling resulted in higher diversity and more rare species than random sampling. This means that estimates of species richness that extrapolate from non-random samples via accumulation curves will also give unreliable predictions of landscape-wide diversity.

Sample size also proved to be an influential aspect, with estimate precision improving when the number of samples increased. The importance of increasing sample size has already been pointed out by Hirzel and Guisan (2002), while Albert *et al.* (2010) argued that sampling design and not sample size is the most relevant factor influencing parameter estimation. Additionally, it has been shown that both configuration and number of sampling points affect beta-diversity estimates, which results in incorrect diversity partitioning estimates (Marsh and Ewers 2013). And even though the present study focuses on alpha diversity, we could also observe that both sample size and sampling design play a significant role, influencing precision and bias, respectively. Therefore, it is advisable to sample the study areas multiple times to reduce uncertainty around the estimates. Nonetheless, this procedure can generate spatial autocorrelation in the residuals. But these can be dealt with using a variety of statistical methods (see Dormann *et al.* 2007).

Finally, we found that the spatial scale determining species richness also changes with sampling habitat. This indicates that the processes affecting diversity actually operate at different scales according to habitat type. For example, the radius best predicting species richness in oilseed rape fields was larger than in semi-natural habitats, what indicates that the landscape-scale dilution effects take place at larger scales as bees spillover to farther areas. This shows that studies that sample only one habitat are valuable to determine how diversity relates to environmental variables or how it increases with area within that habitat type. Nonetheless, it should remain clear that the results will possibly not reflect the response of the whole community if the organisms use resources at larger scales.

CONCLUSIONS

We demonstrated that sampling design can affect the predictability of landscape-wide biodiversity estimates. Our results showed that number of samples per study area affected the precision of parameter estimation and the preferential selection of habitats for sampling generated biased estimates of parameter and species richness. Parameter estimates obtained by sampling in only one habitat type might be relevant when the researcher aims to understand biological responses within the boundaries of the habitat. However, they hardly represent the response of the whole community to the landscape context, since organisms are usually not limited to one habitat type. Caution should be stressed in terms of generalizing too widely from studies performed in a single habitat type. For studies attempting to understand how organisms respond to landscape components, we suggest that the range of the sampling area, variety of sampling habitats and the number of sampling units should be increased to obtain more realistic results.

ACKNOWLEDGMENTS

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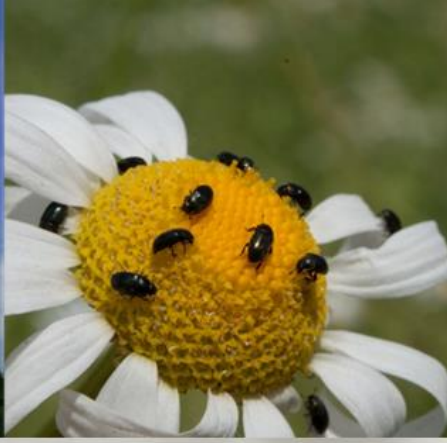
CHAPTER 3

Using multi-level generalized path analysis to understand herbivore and parasitoid dynamics in changing landscapes

Tatiane Beduschi, Teja Tscharntke and Christoph Scherber

ABSTRACT

In patchy environments, such as agricultural landscapes, both spatial and temporal scales of habitat heterogeneity can affect population dynamics and trophic interactions. As a result of crop rotation, landscapes and local resource availability may change dramatically within and between years.

We used a tritrophic interaction constituted by pollen beetles, their host plant oilseed rape (OSR), and their parasitoids, as a model system to investigate how the effect of landscape composition on insect abundance changes with time and whether system dynamics showed carry-over effects of previous years. We employ path analysis models that allow us to study whole networks of hypotheses rather than univariate cause-effect relationships.

We exposed pan traps in a 5x5 grid design within 10 landscapes in June 2011 (after OSR flowering) and May 2012 (at peak OSR flowering). Additionally, we assessed parasitism rates of pollen beetle larvae in May 2011 and measured changes in landscape composition.

The effect of OSR proportion on beetle abundance changed with time from negative (during flowering) to positive (after flowering). Parasitism had a negative effect on the number of newly emerged pollen beetles, but only in landscapes with a low proportion of OSR. Interestingly, our path analysis showed that landscape composition affected herbivore abundance one or two years later, mediated by changes in parasitism.

Our results suggest that plant-herbivore-parasitoid interactions in dynamic agricultural landscapes can show interannual carry-over effects, as they are affected by landscape composition and top-down effects in previous years.

INTRODUCTION

Agricultural landscapes are characterized by fast changes in composition as a result of crop rotations (Wissinger 1997; Thies et al 2005). From an insect herbivore perspective, the availability of suitable host plants may change drastically even within the course of a year (Wissinger 1997).

Effects of landscape context on a given insect herbivore or whole insect communities have been often studied using landscape sectors around individual sampling locations based on sampling only one season (Steffan-Dewenter et al 2002; Chust et al 2003; Tscharntke et al 2005; Concépcion et al 2008; but see Thies and Tscharntke 2008). While these studies have yielded a wealth of insights, they have not evaluated the complex relationships through time and space, but rather focused on only of them.

Both spatial and temporal scales are important to understand trophic interactions and population dynamics (Kareiva et al 1990; Fahrig 1992; Pickett and Cadenasso 1995; Roland and Taylor 1997; Thies et al 2005). Patterns of distribution and abundance of a species might be different when viewed broadly in time and space instead of at a fine scale over a short time period (Wiens et al 1985). Nonetheless, most studies have focused only on the effect of spatial scale and one habitat type. Therefore, in this study, we performed a comprehensive analysis which included a larger temporal scale, replicated in 1x1-km landscape grids. This allowed us to assess a possible carry-over effect, where past years' landscape composition remains influential through long-lasting, interannual effects on insect abundance. Carry-over effects have been observed for soil microorganisms and precipitation (Kardol et al 2007; Reichmann et al 2013), as well as for landscape components that affected the abundance and species richness of solitary bees in the following year (Le Féon et al 2013).

In Central Europe, cropped land is dominated by cereals such as wheat and barley; increasingly, other crops such as maize and oilseed rape are grown. Locally, root crops such as sugar beet are widespread (Eurostat 2013). In addition, most landscapes contain up to 40 percent forest and 10 percent semi-natural habitats such as extensively managed grassland (Keil et al 2010). While amounts of forest and grassland remain relatively stable, cropped land is characterized by strong internal changes in crop identity over time (Rand et al 2006). Many groups of insects, such as pollinators, herbivores or parasitoids, may change in abundance in response to changes in crop composition. In particular, mass-flowering crops such as oilseed rape have been shown to strongly shape insect abundance (Westphal et al 2003; Holzschuh et al 2011).

Oilseed rape (*Brassica napus* L.) is a highly subsidized crop and the increasing demand for the oil produced with its seeds has been followed by an increase in acreage (Alford 2003; BMBF 2012) and a growth of pest populations (Hokkanen 2000). Many pests attack oilseed rape fields, but the pollen beetle (*Meligethes aeneus* F.) is the one that causes the most pronounced negative impacts on oilseed rape flowers (Zaller et al 2008a) and also requires the most control measures (Williams 2010). Due to the different feeding phases, the great capacity of dispersal (Fritzsche 1957) and the possibility of parasitism, pollen beetle abundance can be affected by different landscape components, mainly at large scales (Thies et al 2003; Zaller et al 2008a; Rusch et al 2013a).

Nevertheless, it is still not clear how these components, especially the proportion of oilseed rape, influence beetle abundance. It has remained uncertain if the percent oilseed rape in a landscape is negatively (Zaller et al 2008a), positively (Valantin-Morison et al 2007) or neutrally (Thies et al 2003; Rusch et al 2013a) related to pollen beetle abundance. The discrepancies in the results may arise from unknown differences among the study regions (Rusch et al 2013a), but they could also represent the result of the temporal dynamics in the relationship between pollen beetles, their parasitoids and oilseed rape.

Parasitism rate has been shown to be influenced by soil tillage, insecticide use and landscape composition (Nilsson 1985; Thies and Tscharntke 1999; Ulber et al 2010). While the positive effect of proportion of non-crop has been shown (Thies and Tscharntke 1999; Thies et al 2003; Rusch et al 2011), the role of oilseed rape fields in the surrounding areas is still unclear. Evidence published so far indicates that the proportion of this crop in the previous year could be an important determinant (Thies et al 2008; Rusch et al 2011). However, this possibility has never been directly tested, since the studies considered either the difference in percentage of oilseed rape between years (Thies et al 2008) or the proportion of previous year oilseed rape fields with conventional soil tillage (Rusch et al 2011).

Even though previous studies have investigated how landscape features influence pollen beetle abundance and parasitism, to our knowledge, no study so far has examined the effects on the whole trophic interaction at once. While multiple regression approaches allow deep insights, they may fail in complex interacting systems (Grace et al 2014). Here, we employ generalized multilevel path analysis (Shipley 2000) to study changes in herbivore abundance over time and how it is affected by parasitism in changing landscapes. We used a grid-based sampling approach (following Scherber et al 2012) in 10 replicated landscapes and aimed to answer the following questions:

(1) Is parasitism rate more strongly affected by host plant abundance (proportion of oilseed rape) in the previous or in the current year?

(2) Can we observe a change in the effect of different landscape components on herbivore abundance between the two study years?

(3) Is beetle abundance driven by carry-over effects that span over one or two years?

METHODS

Study system

We used pollen beetle (*M. aeneus*) as a model system because this is one of the numerically most abundant insect herbivores in Central Germany (Ryszkowski et al 2001). Moreover, previous studies have suggested the existence of an interannual effect on this tritrophic interaction (e.g. Thies et al 2008; Rusch et al 2011). The pollen beetle emerges in early spring, after overwintering in the soil of field margins or woodlands, and feeds on pollen of various species of plants before migrating into oilseed rape fields (Nilsson 1988; Williams 2010). They arrive in the fields during bud stage and will feed on pollen by chewing into the buds, where they also oviposit (Nilsson 1988; Cook et al 2004). The main damage caused by pollen beetles happens during the bud stage, since feeding and oviposition cause bud abscission and may reduce yield (Zaller et al 2008b; Williams 2010). The larvae feed on pollen and eventually drop to the soil to pupate. The development from egg to adult takes about one month (Cook et al 2004; Williams 2010). The newly emerged pollen beetles feed on the pollen of different flowers when spring oilseed rape is not available, since the flowering of winter oilseed rape fields will have ended (Hokkanen 2000). Adults of the first generation die after egg laying and, in late summer, the new generation of beetles seek overwintering sites and will only reproduce in the following year (Nilsson 1988, Williams 2010). During the larval stage, pollen beetles are susceptible to attack by specialized parasitoids. The three most common species are *Tersilochus heterocerus* (Thomson), *Phradis interstitialis* (Thomson) and *Phradis morionellus* (Holmgren). The parasitoid egg is laid inside the pollen beetle larvae and hatch once these drop to the soil to pupate (Ulber et al 2010). In the soil, the parasitoid larva completes its feeding and pupates. Parasitoids overwinter as diapausing adults in the soil of the oilseed rape fields and emerge in the following spring (Jourdheuil 1960; Nilsson 2003).

Sampling procedures

Sampling was performed in 2011 and 2012 in 10 landscapes in the surroundings of Göttingen (51°32'N, 9°56'E) in Central Germany. The region mainly consists of cropped land

interspersed with semi-natural non-crop areas like meadows, calcareous grasslands and woodlands. Landscapes were approximately 1km x 1km wide (mean area± SD= 0.93± 0.23km^2) and represented gradients of proportion of winter oilseed rape and non-crop area. Yellow pan traps (150mm x 60mm, 750 ml) were placed at vegetation height throughout each landscape following a 5 x 5 grid and exposed for three days in June 2011 (after oilseed rape flowering) and May 2012 (at peak oilseed rape flowering) in order to collect pollen beetles and their parasitoids. The sampling grid was laid out over the landscapes in such a way to always include forest margins and grasslands (non-crop areas) as well as crop fields, while excluding cities or villages. The number of points located in each habitat type and an example of a sampling landscape can be found in the supplementary material (Table A1 and Fig A1, respectively). Overall, 250 pan traps were exposed per sampling round. Given that some traps were damaged or vandalized, and that a pan trap could only be included in the model when it was present in both years, the final number of samples was 237 per round. The beetles collected when oilseed rape fields were no longer flowering represent mainly the new generation of beetles of 2011 (Williams et al 2007). These beetles were still in their larval stage during oilseed rape blooming and, therefore, could have been attacked by parasitoids. The beetles collected in May 2012 were mature adults that had emerged in the previous year and had overwintered, possibly in nearby forest margins.

In May 2011 (at peak oilseed rape flowering), the flowers of five oilseed rape plants were collected in each grid point located in an oilseed rape field (N= 58) to estimate parasitism rates. Wild flowers in non-crop areas were also inspected, but no pollen beetle larva was found outside oilseed rape flowers. All larvae located within the sampled flowers were counted and, in each sample, 20 individuals were dissected in order to determine the parasitism rate. In the grid points where no larvae were present, the parasitism rate was defined as zero.

Landscape parameters

We used satellite-based image classification to measure proportions of oilseed rape fields and non-crop areas, which include meadows, pastures and forests. Percentage of non-crop area has been shown to be a robust criterion for the quantification of habitat complexity as it tends to be closely correlated with other landscape metrics such as habitat diversity (Thies and Tscharntke 1999). These measurements were done for the years of 2010, 2011 and 2012 and for all study areas using the software ArcGis 10.1 (ESRI Redlands, CA, USA). While proportion of oilseed rape fields changed greatly through time, due to crop rotation, proportion of non-crop area did not change in the studied years. Only winter oilseed rape is considered, given that no spring oilseed rape fields were observed in the study areas or in the surroundings.

According to the literature, pollen beetle abundance and parasitism are affected by landscape components at larger scales, ranging from 750m (Thies et al 2003) to 1250m or larger (Zaller et al 2008). For this reason, we defined a radius of 1000m around each of the 237 sampling points. This value is a mean between the distances reported in the literature and presented a low correlation between explanatory variables (i.e. proportion of oilseed rape and non-crop area, Supplementary Material Table A3).

Data analyses

To evaluate how landscape features and parasitism rates affect pollen beetle abundance over time, we used generalized multilevel path analysis (Shipley 2009). In contrast to classical structural equation modelling, this approach can accommodate nonlinear relationships and non-normal error distributions. Additionally, it is possible to take into account the hierarchical structure of the data, which would, otherwise, violate the assumption of independence among observations.

The model we tested proposes that landscape components affect pollen beetle abundance differently through time both directly and indirectly, through parasitism (Fig 1).
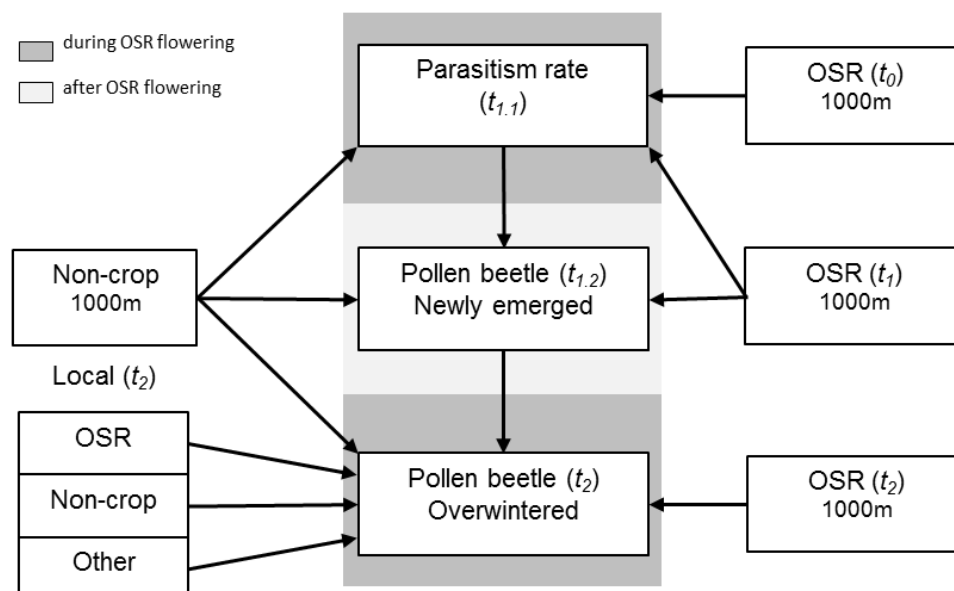
Fig 1. Conceptual structural equation model illustrating hypothesized effects of landscape components on pollen beetle abundance and parasitism through time. "OSR" indicates proportion of area occupied by oilseed rape fields and "Non-crop" the proportion of non-crop area in the surroundings, both within a 1000m buffer from each sampling point. "Local" represents the sampling habitat: non-crop areas (Non-crop), oilseed rape fields (OSR) or other crop fields (Other). Time steps are represented by "t". $t0= 2010$; $t1= 2011$; $t2= 2012$; $t1.1= $ May 2011; $t1.2= $ June 2011.

We hypothesized that parasitism rates in 2011 were affected by proportion of oilseed rape fields in 2010 and 2011 as well as proportion of non-crop area within the 1000m buffer. Moreover, pollen beetle abundance in June 2011 would be determined by parasitism rates in the same year, along with proportion of oilseed rape and non-crop area. These landscape components could also influence pollen beetle abundance in 2012, together with the habitat where each yellow pan trap was located (local scale) and pollen beetle abundance from the previous year. Based on the path diagram constructed following these hypotheses, we generated all possible independence claims, i.e. directional separations (Supplementary Material Table A4). A directional separation (d-sep) comprises a pair of variables that, according to a given path model, are expected to be statistically independent upon conditioning on some other set of variables (Shipley 2000). In order to test the full causal hypothesis represented by the path diagram, we performed a simultaneous test of all four independence claims. That was done by combining the null probabilities of each independence test according to:

$$C = -2 \sum_{i=1}^{k} \ln(p_i)$$

where k is the number of d-sep tests and p_i are the p-values obtained in each d-sep test. Model fit was evaluated by comparing C to a χ^2 distribution with $2k$ degrees of freedom.

The model path coefficients were estimated by fitting generalized mixed models with random intercepts for each sampling landscape. Binomial and Poisson error distributions were used when the response variable was parasitism rate and pollen beetle abundance, respectively. In order to account for overdispersion in the beetle abundance data, we added an observation-level random effect (Elston et al 2001). When used as an explanatory variable, pollen beetle abundance was log transformed to reduce the influence of outliers and to match the log link applied in generalized mixed models. Independence claims were tested in the same way. Interactions were kept in the model when they were both significant ($p<0.05$) and provided an improvement in Akaike's Information Criterion (AIC) higher than 3 (Burnham and Anderson 2002). Residuals were tested for spatial autocorrelation using Moran's Autocorrelation Coefficient (Bivand et al 2008). However, after the inclusion of a random intercept for each landscape, there was no remaining spatial pattern in the residuals. The conditional R-squared was calculated following Nakagawa and Schielzeth (2013). In order to increase clarity, we did not include the correlations between exogenous variables in the model shown in the results section. Those can be seen in the supplementary material (Fig A2) and do not influence the relationships presented in Fig 2.

To establish the determinants of parasitoid abundance in May 2012 (at peak flowering), we fit a linear mixed-effects model. The response variable was log transformed to reduce the influence of outliers and to achieve appropriate distribution of the residuals. The initial explanatory variables were percentage of oilseed rape in 2011 and 2012, percentage of non-crop area around the sampling point and the type of crop (habitat) present in the sampling location in 2011 and 2012. The inclusion of habitat type, while not necessary to answer the proposed question, was important to guarantee the accuracy of the results. The use of attractive yellow pan traps may cause values to be higher in semi-natural habitats and cereal fields during oilseed rape flowering. Therefore, not accounting for the difference between habitat types could have masked the effect of landscape components. The model was simplified to achieve the smallest possible Akaike's Information Criteria (AIC) using forward and backward stepwise selection procedures. According to this method, all parameters remaining after model simplification had relevant explanatory power (Crawley 2013).

All statistical analyses were conducted with R 3.0.2 (R Core Team 2013). To fit the parasitoid abundance model we used the package "nlme" (Pinheiro et al 2013). The hierarchical models were fit using the package "lme4" 1.0-6 (Bates et al 2014). The package "spdep" 0.5-71 (Bivand 2014) was used to calculate the Moran's I. The package "effects" (Fox 2003) was used to create interaction graphs.

RESULTS

Data summary

Percentage of oilseed rape ranged from 0-26% in 2010, 0-45% in 2011 and 0-35% in 2012. Proportion of non-crop area remained almost constant within each area throughout the years varying from 0-73%. Mean pollen beetle abundance per trap was 1180 (SD=±2565; min= 2; max= 33006) in June 2011, and 62.81 (SD=±142; min= 0; max= 1418) in May 2012 (more details can be found in the Supplementary Material Table S3). Mean parasitism rate was 2% (SD=±10%; min= 0%; max= 70%). In May 2012, we collected 501 parasitoids, of which 95.8% were *T. heterocerus*, followed by *P. interstitialis* (2.8%), *P. morionellus* (0.8%) and *Diospilus capito* (0.6%). Since only 7 parasitoids were collected in June 2011, these data were not analyzed.

Path analyses

Effects on parasitism- During oilseed rape flowering (2011)

Even though some paths were not significant, the hypothesized model was well supported by the data (chi-square= 6.01; df= 8; p= 0.64). Proportion of oilseed rape in the previous year ($p<0.001$) and proportion of non-crop area ($p<0.01$) was positively related to parasitism rates, while oilseed rape in the same year had no significant effect (p= 0.54) (Fig 2).
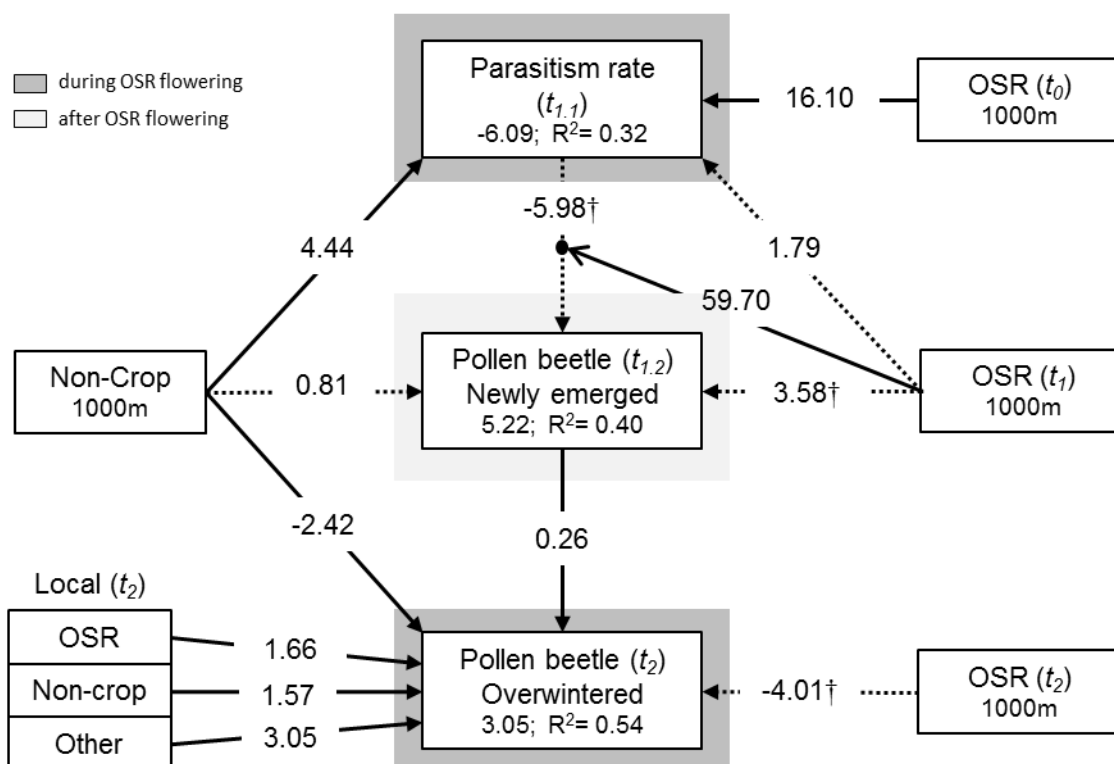

Fig 2. Multilevel path analysis showing effects of different landscapes components on pollen beetle abundance and parasitism through time. "OSR" indicates proportion of area occupied by oilseed rape fields within a 1000m circle. "Non-crop" represents the proportion of non-crop area in the same circle. "Habitat" specifies the local land use where sampling was performed: non-crop areas (Non-crop), oilseed rape fields (OSR) or other crop fields (Other). This model was well supported (chi-square= 10.82, df= 12, p= 0.54). Path coefficients are unstandardized partial regression coefficients obtained from generalized mixed models. Path coefficients explaining parasitism rate are "logit" transformed. All other coefficients are "log" transformed. Arrows ending in other arrows represent interactions. Numbers before semicolons are the model intercepts. Dotted arrows represent non-significant relationships ($p< 0.05$). † denotes marginal significance ($p<0.1$). Time steps are represented by "t". t_0= 2010; t_1= 2011; t_2= 2012; $t_{1.1}$= May 2011; $t_{1.2}$= June 2011.

<u>Effects on newly emerged pollen beetle- After oilseed rape flowering (2011)</u>

Even though parasitism rate and proportion of oilseed rape had marginally significant effects on newly emerged pollen beetle abundance in June 2011 (p= 0.06 and p= 0.09, respectively), only their interaction was significant (p< 0.01). This indicates that parasitism only influenced pollen beetle abundance negatively in landscapes with lower proportions of oilseed rape (Fig 3). Once these proportions were higher, pollen beetle abundance increased with parasitism rate. Proportion of non-crop area did not significantly affect the number of pollen beetles (p= 0.40).
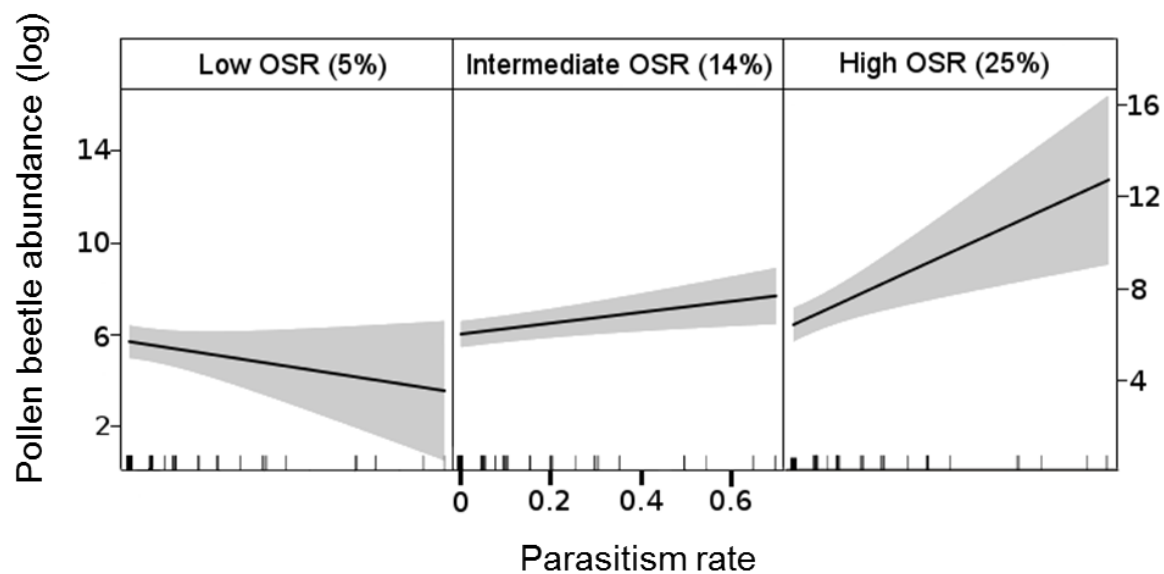

Fig 3. . Effect of the interaction between parasitism rate and proportion of oilseed rape in 2011 on the abundance of newly emerged pollen beetles. From left to right, graphs show low, intermediate and high percentage of oilseed rape within a 1000m radius. Gray-shaded areas represent 95% confidence intervals.

<u>Effects on overwintered pollen beetle- During oilseed rape flowering (2012)</u>

Abundance of newly emerged pollen beetles , in turn, positively affected the number of beetles found in the next year during oilseed rape blooming (p<0.001). Furthermore, this number was negatively affected by proportion of non-crop area (p<0.05) and a strong trend suggested a negative relationship between abundance of overwintered beetles in 2012 and oilseed rape proportion. The sampling habitat influenced the amount of beetles per trap (oilseed rape fields p<0.05; non-crop area p<0.05; other fields p<0.001). In the habitats named "other" (i.e. cereal and beet fields) significantly more beetles were collected in comparison to oilseed rape fields and non-crop area, which presented similar numbers.

Parasitoid abundance

The only remaining parameters in the parasitoid model were the sampling habitats from 2011 and 2012, which means that only these parameters had explanatory power. It was possible to observe that significantly more parasitoids were sampled in former oilseed rape fields, occupied in 2012 by other crops (Fig 4; $p<0.05$). Some parasitoids were also collected in oilseed rape fields, that had been other crops in the year before, but almost no parasitoids were sampled in non-crop areas.
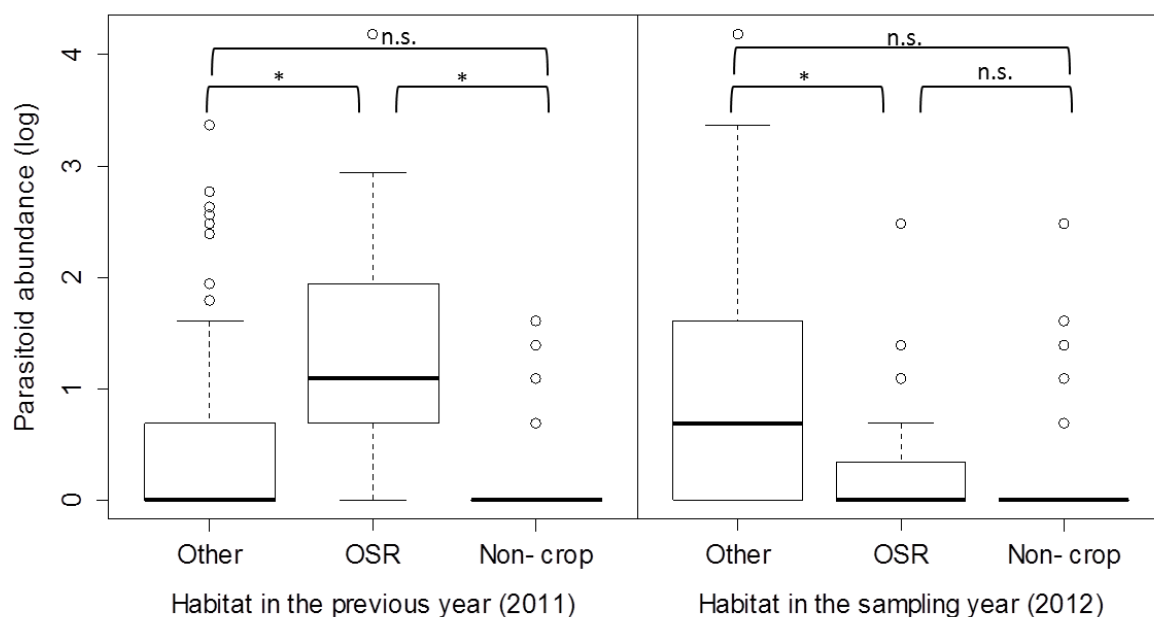
Fig 4. Parasitoid abundance at oilseed rape peak flowering according to the kind of habitat found in the sampling location in the current (right) and in the previous year (left). "OSR" and "Other" represent oilseed rape and other crops (i.e. cereal and beet fields), respectively. Asterisks (*) denote significant differences.

DISCUSSION

Our results show that the effect of oilseed rape fields and non-crop areas on pollen beetle abundance changed with time. Furthermore, the landscape composition had interannual consequences, constituting a carry-over effect.

Landscape components and parasitism rate

The strong positive effect of proportion of oilseed rape in the previous year (2010) on parasitism rates in the following year (2011) had not been directly observed so far. It has been shown that proportion of non-ploughed oilseed rape fields from the previous year can be an important determinant of parasitism rate (Rusch et al 2013a) but, although all the fields in our

study site were ploughed, this parameter still had the greatest effect. This is probably due to the fact that parasitoids of pollen beetles overwinter in oilseed rape fields (Jourdheuil 1960). The positive relationship between non-crop area and parasitism rate concurs with the literature (Thies and Tscharntke 1999; Thies et al 2003; Rusch et al 2011). The lack of ploughing in these environments may enable parasitoid populations to build up over years (Nilsson 1985; Thies et al 2003). Likewise, these areas might provide alternative hosts or additional nectar resources (Frenzel and Brandl 1998; Wratten and Van Emden 1995). This supplementary food supply could facilitate the migration from hibernation sites to oilseed rape fields, given that, after hatching, the parasitoids are very limited in energy (Nilsson 2003; Rusch et al 2013b).

Moreover, it is important to notice that parasitism rates were generally low, as was parasitoid abundance in 2011. This is possibly a consequence of the use of insecticides that year, which was intensified due to the high abundance of pollen beetles. It has been reported that insecticides can reduce parasitoid abundance by approximately 50% and, therefore greatly affect parasitism rates (Ulber et al 2010).

Effects of parasitism rate and oilseed rape on newly emerged pollen beetles

Even though proportion of oilseed rape in 2011 did not affect parasitism rate, it did influence its efficiency. Parasitism rates only had a negative effect on subsequent abundance of newly emerged pollen beetles (2011) when the current proportion of oilseed rape in the landscape was low. Once the prevalence of this crop increased, pollen beetle abundance was positively related to parasitism rates. Similar results were reported by Gladbach et al (2010), who found a positive relationship between pollen beetle larval abundance and parasitism rate and there are two reasons why it could be happening. The first is that parasitoids follow olfactory and visual cues coming from oilseed rape fields and are specially attracted by plants infested with pollen beetle (Williams et al 2007; Jönsson and Anderson 2007) and the second is that the probability of a female encountering a host larva can increase with host density (Williams and Cook 2010). Our study indicates that proportions of oilseed rape play a more important role in increasing pollen beetle offspring than parasitism in reducing it. This is possibly because a higher abundance of host plants can reduce intraspecific competition among pollen beetle larvae (Hokkanen 2000), accounting for the higher number of newly emerged pollen beetles in areas with higher proportions of oilseed rape.

Landscape components and overwintered pollen beetles

Conversely, during blooming the relationship between the proportion of oilseed rape in the current year and overwintered pollen beetles (2012) was negative. Even though oilseed rape

fields attract pollen beetles (e.g. Williams et al 2007, Williams and Cook 2010) it seems that, during flowering, the local pest pool, formed by the beetles that overwintered within the landscape, is an important limiting factor of pollen beetle abundance. The strong dilution trend caused by oilseed rape area also indicates that in spite of the potential of large oilseed rape areas to attract overwintered beetles from other landscapes, the populations were not large enough to exploit fully the short-term increase in flower resources. The negative influence of non-crop habitats on abundance of overwintered beetles could also represent a weaker dilution effect, as they would also spillover to these areas. Pollen beetles respond not only to volatiles emitted by oilseed rape but also to the odour of several plant species, including rye (*Secale cereale* L.) (Ruther and Thiemann 1997), and are often found in wild flowers (Ahmed et al 2013; Honěk et al 2013). Additionally, almost the same number of overwintered beetles (2012) was collected in oilseed rape and in non-crop areas, and even more were found in other crops. Given the attractiveness of the yellow pan traps, these results do not represent local abundance of pollen beetles, but provide evidence that these herbivores will spillover from oilseed rape fields to surrounding habitats when a stimulus is provided. These results contrast with those of Gladbach et al (2010) who found spillover from oilseed rape onto wild cruciferous plants only for parasitoids, but not pollen beetles. Possibly, this difference arises from the fact that in their study, only larvae sampled after flowering were considered and not adults. Once the oilseed flowers have faded, the number of adults and larvae can be uncorrelated, since many of the adults are newly emerged and unable to reproduce and most of the larvae will have already dropped to the soil to pupate (Williams et al 2007; Williams 2010).

Overall, our study indicates that percentage of oilseed rape in the landscape can be an important driver of pollen beetle abundance. This is in line with a series of other studies (Valantin-Morison 2007; Zaller et al 2008a), but in contrast to Rusch et al 2013a, in which proportion of oilseed rape fields was considered to be much less relevant than non-crop area. In their study, sampling took place while oilseed rape fields were in the bud stage, when pollen beetles are still emerging from overwintering sites (i.e. non-crop area) and can still be largely influenced by the proportion of these sites. In our study, sampling was performed only during and after flowering.

Carry-over effects of landscape components

Our results showed an interannual carry-over effect of landscape components. For example, percentage of oilseed rape in 2010 affected overwintered pollen beetle abundance in 2012 by increasing parasitism rates in 2011 and, consequently, reducing the new generation of

that year. These new beetles then partly comprised the pollen beetle population in the following year.

Given that agricultural landscapes are prevalent in Central Europe (Keil et al 2010), this kind of carry-over effect from landscape components could commonly influence insect populations that benefit from farming areas. Recent history of land use has been shown to affect solitary bee diversity and abundance (Le Féon et al 2013), as the inclusion of grasslands in crop rotation promoted a durable benefit to the bee community. Long lasting effects of landscape components can possibly also be observed in other pest populations, such as aphids, which are affected by processes acting at landscape scale (Thies et al 2005).

The scale at which these effects can be observed will probably depend on the mobility of the organism and on landscape configuration. For example, in more compartmented regions, covered by large semi-natural habitats in one part and cropped land in the other, regional scale migrations of the mobile pollen beetles can occur (Rusch et al 2013a). This would increase the spatial scale of the interannual carry-over effects or possibly overthrow them.

Recommendations for landscape managers

We propose that breaking off oilseed rape cultivation in a large area for one year, as suggested by Ekbom (2010), would be a more efficient strategy to control pollen beetles than keeping oilseed rape area constant (Zaller et al. 2008b, Frank et al 2010). Avoiding dramatic fluctuations in oilseed rape area would probably enable the beetle population to build up through time, while the approach proposed by Ekbom (2010) could dramatically reduce the number of new generation beetles. Given that parasitoids would also be negatively affected, it is recommendable to create "parasitoid conservation" areas containing a less preferred host plant species, such as white mustard. With this setting, pollen beetles would be allowed to lay eggs and parasitoids could reproduce. Ideally, such areas would be placed near to fields expected to have overwintering parasitoids.

CONCLUSIONS

We found that the effect of oilseed rape on pollen beetle abundance changed with time. It was negative during flowering on overwintered beetles and positive after flowering on new generation beetles. Additionally, it was possible to observe a carry-over effect of oilseed rape, given that the proportion of this crop in 2010 indirectly affected the abundance of overwintered pollen beetles in 2012. This effect was mediated by changes in parasitism rates, which then affected the abundance of newly emerged pollen beetles. Carry-over effects of landscape

components could affect other insect populations in agricultural areas, but further studies are necessary to define how prevalent these effects are in other landscapes and organisms. Our study showed that parasitoid-host interactions and the host's population dynamics can be much more complex in the annually changing cropped land landscapes than usually thought. Generalized multilevel path analysis can be an important tool to study such cascading effects, given that this approach allows the analyses of networks of causal processes, while bivariate analyses are limited to simpler models (Grace et al 2014).

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SUPPLEMENTARY MATERIAL

Table A1. Number of sampling points per habitat type in each study year.

Habitat	2011	2012
Semi-natural habitats	78	72
Oilseed rape fields	58	35
Other	109	130
Total	245	237

Table A2. Mean number of pollen beetles per habitat type per year. Standard deviations are shown inside brackets.

Habitat	After flowering (2011)	During flowering (2012)
Semi-natural habitats	1597.44 (4353.11)	17.70 (31.83)
Oilseed rape fields	1643.29 (1537.64)	7.28 (7.68)
Other	664.57 (730.49)	102.75 (181.88)

Table A3. Pearson's correlation coefficients (below diagonal), variances (diagonal, bold type) and covariances (above diagonal).

Variable	PB 2011	PB 2012	Parasitism	OSR (2010)	OSR (2011)	OSR (2012)	Non-crop
PB 2011	**2.223**	0.441	0.033	-0.017	0.019	-0.027	0.054
PB 2012	**0.174***	**2.880**	0.021	-0.011	0.060	-0.015	-0.085
Parasitism	0.227*	0.126	**0.010**	0.000	0.000	-0.001	0.002
OSR (2010)	-0.173*	-0.099	0.042	**0.004**	-0.002	0.000	-0.0018
OSR (2011)	0.143*	0.404*	0.017*	-0.389	**0.007**	-0.001	-0.003
OSR (2012)	-0.259*	-0.132*	-0.133*	0.055	-0.080	**0.004**	-0.002
Non-crop	0.260*	-0.360*	0.125	-0.199*	-0.240*	-0.220*	**0.019**

OSR- proportion of oilseed rape within a 1000m radius around each sampling point in 2010, 2011 and 2012. Non-crop- proportion of non-crop area in the same radius. PB- pollen beetle abundance (log transformed) in 2011 and 2012. Parasitism- parasitism rates in May 2011.
Asterisks (*) indicate significant results ($p<0.05$).

Table A4. Directional separation test (d-sep) of conditional independence implied by our conceptual model (Fig.1).

D-sep claim of independence	Model formula	*p* value
$(X_2; X_6) \mid \{X_5, X_8, X_7, X_3, X_1, X_4\}$	$X_6 \sim \mathbf{X_2}* X_3 + X_8 + X_7 + X_1 + X_5 + X_4$	0.37
$(X_3; X_6) \mid \{X_5, X_8, X_7, X_4\}$	$X_6 \sim \mathbf{X_3} + X_7 + X_8 + X_5 + X_4$	0.59
$(X_1; X_6) \mid \{X_5, X_8, X_7, X_4\}$	$X_6 \sim \mathbf{X_1} + X_7 + X_8 + X_5 + X_4$	0.79
$(X_1; X_5) \mid \{X_2, X_3, X_4\}$	$X_5 \sim \mathbf{X_1} + X_2* X_3 + X_4$	0.28
$(X_3; X_8) \mid \{\varnothing\}$	$X_8 \sim \mathbf{X_3}$	0.22
$(X_1; X_3) \mid \{\varnothing\}$	$X_3 \sim \mathbf{X_1}$	0.42

X1 = proportion of rape in a 1000m buffer in 2010, X2 = parasitism rate in May 2011, X3 = proportion of rape in a 1000m buffer in 2011, X4 = proportion of non-crop area in a 1000m buffer, X5 = abundance of pollen beetles in June 2011, X_6= abundance of pollen beetles in May 2012, X_7= sampling habitat, X_8= proportion of rape in a 1000m buffer in 2012.

'Model formula' refers to the associated mixed model regression for each d-sep claim using the glmer or the lme function in R; the grouping variable, fitted as random intercept, are the 10 sampling areas.

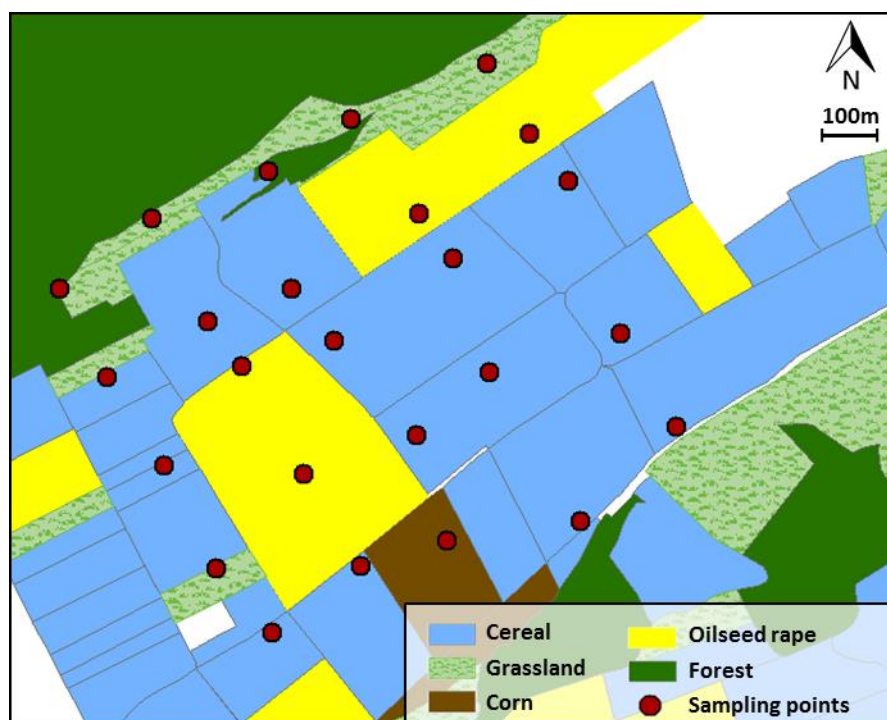The variables in bold are those whose partial regression coefficients should be zero ($p> 0.05$).

Fig A1. Example of a sampling landscape (Lengden; 51°30'14".00 N, 10°01'22'.42 O). White areas represent settlements.
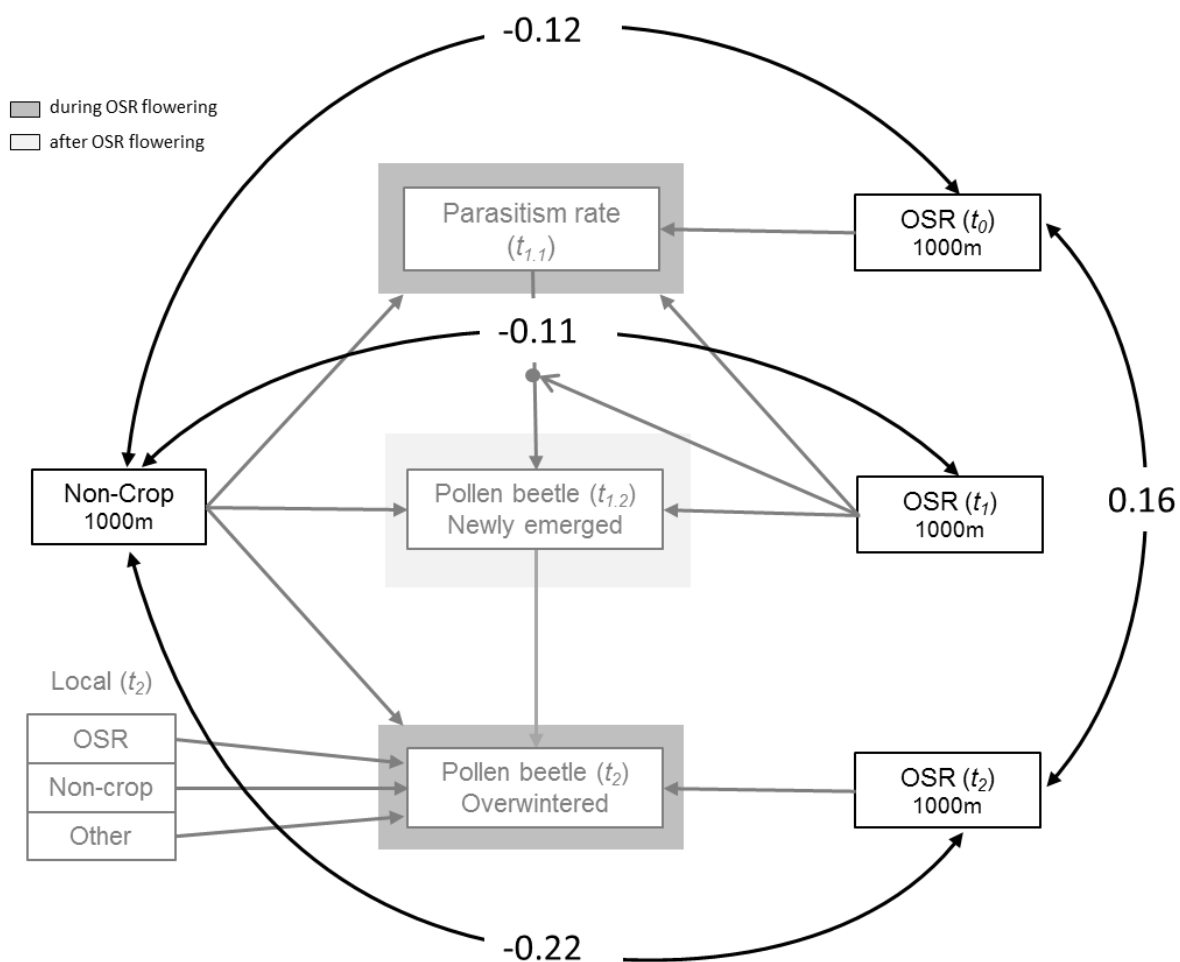
Fig A2. Complement of the multilevel path analysis showing the relationship between exogenous variables. Relationships not shown were not significant and are included in the independence tests. Analyses were performed following Shipley (2003). "OSR" indicates proportion of area occupied by oilseed rape fields and "Non-crop" the proportion of non-crop area in the surroundings, both within a 1000m buffer from each sampling point. "Local" represents the sampling habitat: non-crop areas (Non-crop), oilseed rape fields (OSR) or other crop fields (Other). The indicators "t0", "t1" and "t2" represent three different years, while "t1.1" and "t1.2" denote two different periods from the same year ("t1").

Shipley, B. (2003) Testing recursive path models with correlated errors using d-separation. Structural Equation Modeling, 10(2), 214-221.

R SCRIPT

```
library(lme4)
library(nlme)


###### Independence tests


fit1<- glmer(pb.2012~log(pb.2011+1)+ local.habitat.2012+
prop.OSR.2012+ prop.OSR.2010+ prop.OSR.2011* parasitratio+
prop.SNH+(1|area)+(1|Unit), family=poisson,data=semdata,
na.action=na.omit)


fit2<- glmer(pb.2012~log(pb.2011+1)+ prop.OSR.2012+
local.habitat.2012+ prop.OSR.2011+ prop.SNH+ (1|area)+ (1|Unit),
family=poisson, data=semdata, na.action=na.omit)


fit3<- glmer(pb.2012~log(pb.2011+1)+ prop.OSR.2012+
local.habitat.2012+ prop.SNH+ prop.OSR.2010+ (1|area)+ (1|Unit),
family=poisson, data=semdata, na.action=na.omit)


fit4<- glmer(pb.2011~ parasitratio* prop.OSR.2011 + prop.SNH+
prop.OSR.2010+ (1|area)+(1|Unit),family=poisson, data=semdata,
na.action=na.omit)


fit5<- lme(prop_rape_1000m~rape1000_prop_10, random=~1|area,
data=semdata, na.action=na.omit)


fit6<- lme(prop_rape_1000m_12~prop_rape_1000m, random=~1|area,
data=semdata, na.action=na.omit)


summary(fit1)
summary(fit2)
summary(fit3)
summary(fit4)
summary(fit5)
summary(fit6)


fisherC<- -2*(log(0.37)+log(0.59)+log(0.79)+log(0.28)+ log(0.42)+
log(0.22))
1-pchisq (fisherC,12)
```

```
###### Model fits

parasitism<- glmer(cbind(parasit,not_parasit)~ prop.OSR.2010+
prop.SNH+ prop.OSR.2011+(1|area), data=semdata, family=binomial)
    pollen.beetle.2011<- lme(log(pb.2011+1)~ prop.SNH+
parasitratio*prop.OSR.2011, random=~1|area, data=semdata,
na.action=na.omit)
    pollen.beetle.2012<- glmer(pb.2012~ log(pb.2011+1)+
local.habitat.2012+ prop.SNH+ prop.OSR.2012+(1|area)+(1|Unit),
data=semdata, family=poisson, na.action=na.omit)


###### Relationship between exogenous variables

OSR2010.SNH<- lme(prop.OSR.2011~ prop.SNH, random=~1|area,
data=semdata, na.action=na.omit)
    OSR2011.SNH<- lme(prop.OSR.2011~ prop.SNH, random=~1|area,
data=semdata, na.action=na.omit)
    OSR2010.SNH<- lme(prop.OSR.2010~ prop.SNH, random=~1|area,
data=semdata, na.action=na.omit)
    OSR2012.OSR2010<- lme(prop.OSR.2012~ prop.OSR.2010, random=~1|area,
data=semdata, na.action=na.omit)


###### Variables

prop.OSR.2010= proportion of oilseed rape within a circle of 1000m
around each sampling point in 2010
    prop.OSR.2011= proportion of oilseed rape within a circle of 1000m
around each sampling point in 2011
    prop.OSR.2012= proportion of oilseed rape within a circle of 1000m
around each sampling point in 2012
    prop.SNH= proportion of semi-natural habitats within a circle of
1000m around each sampling point
    parasitratio= proportion of parasitized larvae
    parasit= number of parasitized larvae
    not_parasit= number of not parasitized larvae
    local.habitat.2012= sampling habitat in 2012 (semi-natural habitats,
oilseed rape fields or other crop fields)
    pb.2011= number of pollen beetles in each trap in 2011
    pb.2012= number of pollen beetles in each trap in 2012
    area= each of the 10 sampling landscapes
```

CHAPTER 4

Semi-natural habitats increase spatial similarity of pollinator communities within agricultural mosaic landscapes

Tatiane Beduschi, Teja Tscharntke, Urs Kormann and Christoph Scherber

ABSTRACT

Community similarity and small-scale species sorting in agricultural landscapes, composed of a mosaic of cropland and grassland patches can be expected to change with habitat type and distance to habitats providing resources. Although landscape context has been shown to influence community structure, studies so far neglected potential spatial changes in community composition of functional groups. In this study, we assessed how spatial turnover of pollinator communities is influenced by landscape context in agricultural areas.

We compared solitary bees and hoverflies, both of which are important pollinator groups, yet often show contrasting responses to landscape context. We sampled whole landscapes and assessed how the relationship between community dissimilarity and spatial distance is affected by the proportion of mass flowering crops (oilseed rape, OSR), providing large amounts of floral resources during blooming, and semi-natural habitats (SNH), supplying resources more continuously over the season. While the proportion of OSR did not explain spatial community turnover for either taxon, SNH had a homogenizing effect on bee communities during OSR flowering and on hoverfly communities after flowering. The transience of the effect indicates that this pattern was caused by exchange of individuals between habitats. Larger proportions of SNH could facilitate the movement between foraging and oviposition habitats, thus contributing to increase similarity among local assemblages. Community homogenization and reduction of species turnover are often described as detrimental. However, increased spillover of pollinators between habitats can expand the access to resources that are continuously available over the season and may ensure more predictable pollination service.

INTRODUCTION

Agricultural landscapes comprise 40% of the global land's surface (Martin et al. 2012; Foley et al. 2005), which makes the maintenance of biological diversity in such landscapes crucial for sustaining biodiversity worldwide (Tscharntke et al. 2005; Fahrig et al. 2011). There is a rich literature investigating how agricultural intensification may affect biodiversity, and many of these studies consider the effect of landscape context on species richness. However, this measure of diversity does not consider community composition, which can change substantially, often resulting in a decline of more sensible species (Laurance et al. 2000; Carré et al. 2009; Tscharntke et al. 2012). Additionally, the few studies that assess the relationship between agricultural intensification and community structure at landscape scale ignore spatial distance between communities or regard it as an inconvenient variable that should be removed from the analyses (Liebhold and Gurevitch 2002; Soininen et al. 2007). Spatial dispersal processes have been shown to be an important factor structuring communities and should be explicitly included in the analyses (Cottenie 2005). This is especially relevant in agricultural landscapes, which are unstable environments characterized by heterogeneous habitat patches and fast changes in composition due to harvest and crop rotation (Wissinger 1997; Thies et al. 2005; Thies et al. 2008). Therefore, communities in such landscapes are formed by assemblages that occupy highly dynamic habitats, which cause species to be strongly affected by traits associated to spatial dynamics such as dispersal (Harrison and Taylor 1997; Leibold et al. 2004). This happens because organisms move between natural habitats, which offer spatiotemporal stability of resource availability, and temporary crop habitats containing larger concentrations of their required resources (Tscharntke et al. 2012). Cross-habitat spillover depends on the dispersal ability of the species and tends to be restricted for organisms with limited dispersal (Tscharntke and Brandl 2004; Tscharntke et al. 2012).

We compared solitary bees and hoverflies, which show contrasting responses to landscape structure due to distinct resource requirements and dispersal abilities (i.e. foraging ranges) (Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2002; Holzschuh et al. 2008). Solitary bees have a small foraging range, given that they have to commute between nesting and feeding sites in order to collect pollen for their offspring, and hence require nesting and foraging habitats to be near (Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2002). Hoverflies, on the other hand, have no need to return to the oviposition sites and may disperse over longer distances (Jauker et al. 2009; Raymond et al. 2013). Additionally, hoverflies are often more generalist than bees with respect to floral resources (Biesmeijer et al. 2006), and most of

their larval prey is found in arable fields (Meyer et al. 2009), which causes this taxon to be less disturbed by agricultural intensification or to even benefit from it. Thus, even though bees are more efficient pollinators (Jauker et al. 2012), hoverflies may play a significant role in sustaining pollination services in agricultural areas unsuitable for specialized or less mobile bee species (Jauker et al. 2009; Hänke et al. 2014).

Increasing pollinator diversity throughout the landscape is important to increase temporal and spatial stability of pollination (McCann 2000; Garibaldi et al. 2011). Pollinator populations are known to be highly variable across space and time (Williams et al. 2001), and a diverse set of species can guarantee pollination for crops and wild plants (Kremen et al. 2002). Higher pollinator species richness can also increases fruit set, meet the pollination requirements of a greater number of crops and provide insurance in the event of shortages of any individual species (Kremen et al. 2002; Garibaldi et al. 2013).

In this study, we use a grid-based sampling approach to sample pollinating insects in whole landscapes and assess how landscape context affects landscape-wide spatial community turnover. Sampling pollinators in different habitat types nested in the same species pool allows us to investigate the drivers of community dissimilarity between local assemblages. In particular, we investigate two habitat types that potentially shape pollinator abundance and diversity: Semi-natural habitats and mass flowering crops. Semi-natural habitats such as grasslands managed with low intensity provide continuous food and nesting resources over the season (Steffan-Dewenter et al. 2002). Further, we assess the potential effects of locally abundant mass-flowering crops (oilseed rape) and study potential effects of temporary pollinator dilution in nearby areas (Holzschuh et al. 2011).

We test the following hypotheses:

(1) Spatial community turnover within landscapes is affected by landscape context, i.e. proportion of semi-natural habitats and/or of oilseed rape fields, due to altered species exchange between local communities (Fig. 1).

(2) Hoverfly communities are generally more homogeneously distributed throughout the landscape and are, therefore, less affected by landscape context than solitary bees.

(3) During the flowering period, spatial community turnover is driven by the proportion of oilseed rape fields. Semi-natural habitats and other crop fields have a more relevant role for bees and hoverflies after blooming.
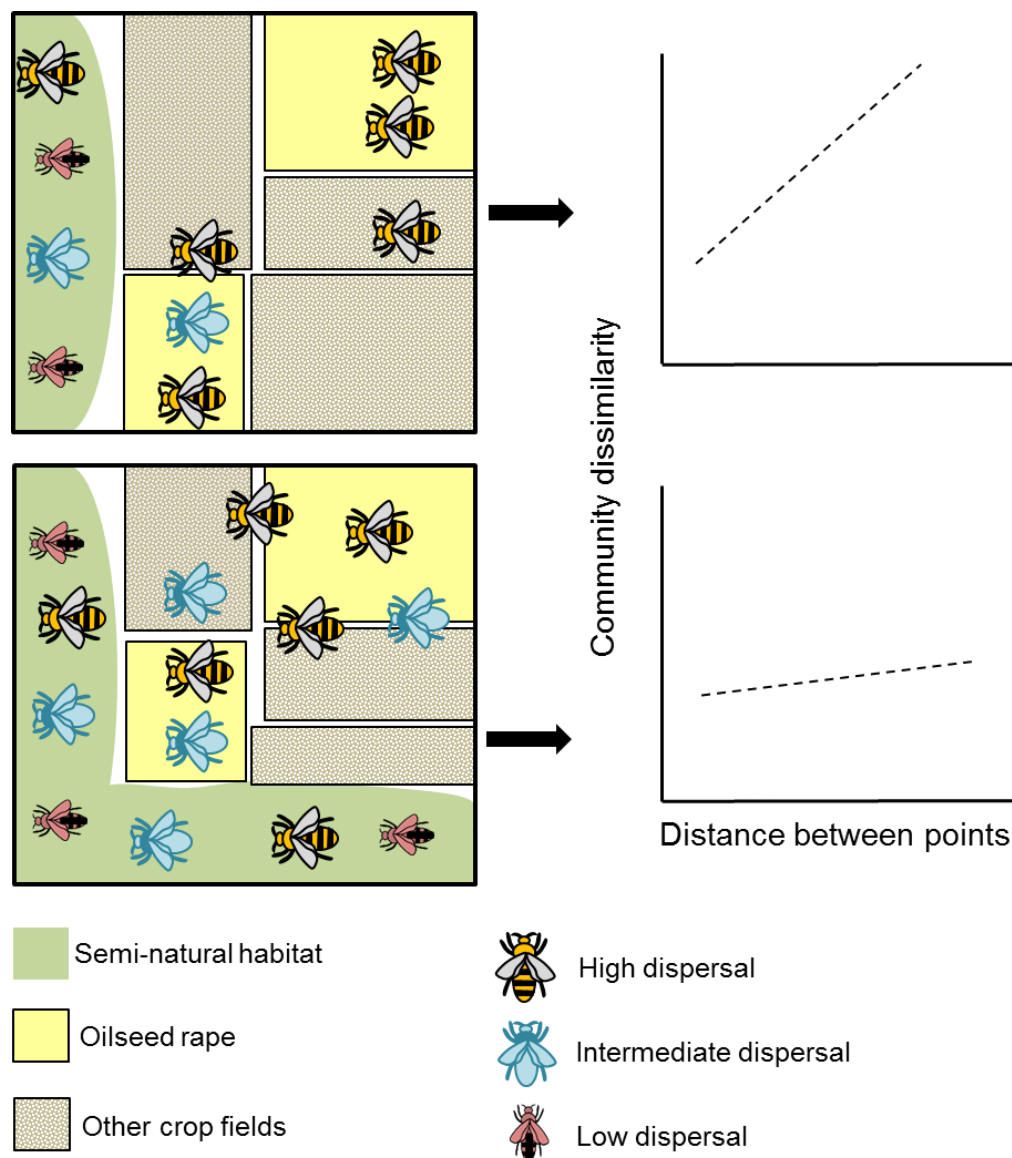
Fig 1. Example of the hypothesized effect of proportion of semi-natural habitats on spatial turnover between local assemblages of bees. It shows how the exchange of individuals among habitat types could reflect on the relationships between distance and community dissimilarity index. One correlation coefficient was obtained per site in each round and year (n=40) and these values were used as response variables in the spatial community turnover models. (a) represents a landscape with low proportion of semi-natural habitats (meadows, pastures or forest margins). In this scenario, bees with low or intermediate dispersal abilities (central place foragers) are limited to semi-natural habitats or their surroundings and cannot explore resources in the farther end of the landscape, which are only accessible to bees with larger foraging ranges. This would generate a higher correlation coefficient for the community dissimilarity-distance relationship. (b) represents a landscape with high proportion of semi-natural habitats. In this case, there are more resources in arable fields within foraging distance and bees with low or intermediate dispersal abilities can be present in a larger proportion of the landscape. This would generate a smaller correlation coefficient for the community dissimilarity-distance relationship.

METHODS

Sampling procedures

The study was conducted in the surroundings of Göttingen (51° 32' N, 9° 56' E) in Central Germany. The region is dominated by intensive agriculture interspersed with semi-natural non-crop areas like meadows, calcareous grasslands and woodlands (Steffan-Dewenter et al. 2002). The sampling landscapes were approximately 1km x 1km wide (mean area± SD= 0.93± 0.23km^2) and represented gradients of percent area occupied by oilseed rape fields and semi-natural habitats (for more details on the gradients see Supplementary Material Table A3). In each landscape, we sampled according to a 5x5 grid, following the approach suggested by Scherber et al. (2012). The grid was laid out over the landscapes in such a way to always include forest margins and grasslands (semi-natural habitats) as well as crop fields, while excluding cities or villages.

At each of these 25 points per landscape, we sampled pollinators with yellow pan traps, filled with water and placed at vegetation height. Traps were exposed for three days in four periods: May 2011 and 2012 (during oilseed rape flowering) and June 2011 and 2012 (after oilseed rape flowering).

Out of 1000 samples (10 landscapes × 25 traps × 4 sampling periods), 29 resulted from damaged traps and thus had to be omitted from the analyses. All wild bees and hoverflies were determined to species level by specialists. Sampling habitats included oilseed rape fields, semi-natural habitats (grasslands or forest margins), and other crop fields (mainly cereal, corn and sugar beet fields). Satellite-based image classification was used to measure the proportion covered by oilseed rape fields, semi-natural habitats and other fields for each landscape and year separately. Satellite imagery was provided by RapidEye™ and image classification was performed using ENVI EX® and ESRI® ArcMap™10.

Community similarity and spatial distance

To quantify the dissimilarity-by-distance relationship for each landscape, we first calculated a matrix of pairwise community dissimilarities between sampling points for each landscape and sampling period separately. There is a great variety of community similarity measures, which vary in the degree of importance on presence/absence, relative abundance and the inclusion vs. exclusion of joint absences (Anderson et al. 2011). Here, we used Bray–Curtis dissimilarity which includes both species composition and relative abundance. This makes sense as not only the species richness, but also the relative abundance of pollinators can be affected

by landscape composition. Nonetheless, alternative dissimilarity measures strongly correlated with the Bray-Curtis index (Chao r=0.95 and Raup Crick r=0.92). Spatial distance was calculated for each pair of sampling points using Euclidean dissimilarities. To assess the within-site spatial community turnover, we tested the relationship between the Bray-Curtis dissimilarity and Euclidean distance at the plot level. This was done using a Mantel test with Spearman's rank correlation coefficient. This allowed us to measure how the difference in species composition between two points is related to their distance to each other. This was done for each site in each sampling period. The more dissimilar species composition become with distance between sampling points, the more heterogeneous the sites are, since species may be concentrating in patches (Fig. 1). Therefore, the correlation coefficients obtained in the Mantel tests could be used as a measure of heterogeneity between local assemblages within landscapes.

Statistical analyses

Statistical analyses were done on two spatial scales: (1) on a large scale, to test the effect of landscape components on the correlation coefficients of the dissimilarity-distance relationship, we performed linear mixed-effects models with Gaussian error distribution. The response variable was the correlation coefficient of the dissimilarity-distance relationship and the explanatory variables were year (as a categorical variable), proportion of oilseed rape fields as well as proportion of semi-natural habitats in each landscape. We also included a random intercept for each sampling landscape. Since we expected the communities to react differently to the landscape variables during and after oilseed rape flowering (high availability versus no availability of mass flowering ressources), we performed two different models: one for samples collected in during oilseed rape flowering (May 2011 and 2012), and another for samples collected after oilseed rape flowering (in June 2011 and 2012). Model selection was done using backward stepwise selection in order to achieve the lowest possible Akaike's Information Criterion (AIC) (Crawley 2013), corrected for small sample sizes (i.e. employing AICc rather than AIC, Burnham and Anderson 2002).

(2) On a smaller scale, to compare local (i.e. per trap) species richness between habitats, we applied generalized linear mixed-effects models with Poisson error distribution, which is adequate for count data. The response variable was the number of species in each plot and the explanatory variables were year and the habitat type where sampling was performed (semi-natural habitat, oilseed rape field or other crop fields). A random intercept for each sampling landscape was used and different models were performed for during and after oilseed rape flowering. Maximal models were simplified in a manual stepwise backward selection on the

basis of AIC values. Variables were kept in the model when they provided a decrease in ΔAIC of more than 3 (Burnham and Anderson 2002).

All statistical analyses were conducted with R 3.0.2 (R Core Team 2013). Models were fit using the packages *nlme* (large spatial scale; Pinheiro et al. 2013) and *lme4* (small spatial scale; Bates et al. 2014). Residual spatial autocorrelation was assessed for both small and large scale models using Moran's Autocorrelation Coefficient (Bivand et al. 2008) and the package *spdep* 0.5-71 (Bivand 2014), but no remaining spatial pattern was found. Stepwise selection was performed using the *stepAIC* function from the *MASS* package (Venables and Ripley 2002), corrected for small sample sizes (i.e. employing AICc rather than AIC; Burnham and Anderson 2002).

RESULTS

Data summary

We collected a total of 3526 hoverfly individuals representing 67 species, as well as 93 bee species with 5241 individuals. Species lists are available in the supplementary material (Appendix 1, Tables A1 and A2). In both years, most individuals were collected after oilseed rape flowering (79% of the bees and 96% of the hoverflies).

Table 1. Results of the generalized linear mixed models relating species richness at plot level (local) and habitat type. Effect of year is shown when decreased model AIC by at least 3. Model coefficients and the respective standard error of the mean (between brackets) are given. Intercepts were removed from the models in order to obtain the mean value of species richness per habitat type. Values were exponentially back transformed. Habitat types are: semi-natural habitats (SNH), oilseed rape fields (OSR) and other crop fields (Other).

Period	Taxon	SNH	OSR	Other	Year
During flowering	Bees	1.75 (1.09)	0.86 (1.12)	1.34 (1.09)	-
	Hoverflies	0.44 (1.24)	0.06 (1.61)	0.17 (1.28)	-1.03 (0.15)
After flowering	Bees	2.29 (1.09)	1.73 (1.11)	2.53 (1.10)	-0.16 (0.04)
	Hoverflies	2.69 (1.06)	3.56 (1.08)	3.97 (1.07)	-2.04 (0.17)

Table 2. Total number of species sampled in each habitat type during and after flowering (mean between years). "Overall" denotes the number of species sampled in each habitat type when all four sampling periods were pooled. Habitat types are: semi-natural habitats (SNH), oilseed rape fields (OSR) and other crop fields (Other).

Period	Taxon	SNH	OSR	Other
During flowering	Bees	35	16	30
	Hoverflies	12	2.5	9
After flowering	Bees	32	15	35
	Hoverflies	22	16	25
Overall	Bees	73	38	69
	Hoverflies	46	28	44

Species richness (Local scale)

While total hoverfly species richness at local scale was always higher on "other" fields such as cereals, corn and sugar beet (Table 1, Fig. 2), bee species richness was higher in semi-natural habitats during oilseed rape flowering and in "other" crop fields afterwards (Table 1, Fig. 2). When both sampling periods were pooled, more species were found in semi-natural habitats than in crop fields, both for bees and hoverflies (Table 2). Generally, more insects were collected in the first year than in the second. This difference was less important for bees than hoverflies, but year was always present in the final models.
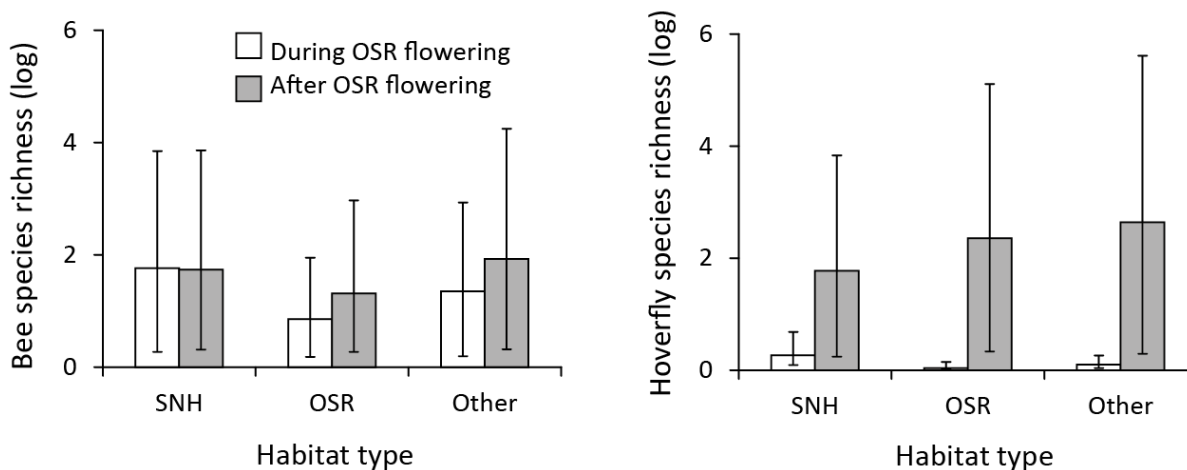

Fig 2. Mean bee and hoverfly number of species observed in each plot during and after oilseed rape flowering in semi-natural habitats (SNH), oilseed rape fields (OSR) and other crop fields (Other). Values were obtained from a generalized linear mixed model with "sampling landscape" as a random intercept. Error bars represent 95% confidence intervals.

Heterogeneity between local assemblages (Landscape scale)

As hoverflies were not sufficiently abundant *during* oilseed rape flowering, community similarity could not be calculated for most landscapes. Therefore, we only estimated the effect of landscape composition on the spatial community turnover for hoverflies *after* flowering.

The mantel correlation coefficient decreased with increasing proportion of semi-natural habitat (Fig. 3, Table 3). This indicates that spatial distance between traps explained differences in community similarity well at low but not at high landscape level amounts of semi-natural habitat. That was the case for bees during oilseed rape flowering (Fig. 3) and for hoverflies after flowering (Fig. 3). Proportion of oilseed rape could not explain the observed patterns at any time and for either taxon (Table 3). Year was only an important for hoverflies after flowering (Table 3).

Nonetheless, it was possible that the effect of semi-natural habitats would have arisen from a "sampling artifact". This means that, in landscapes with a higher proportion of semi-natural habitats, more samples would belong to this same habitat and this would decrease dissimilarity between local assemblages, since we would more often be comparing the same habitat type. To eliminate the possibility of this sampling artifact we performed the same analysis with a limited number of samples from semi-natural per landscape. Notwithstanding, this did not change the observed patterns (for more details see Supplementary Material, Section "*Effect of number of samples in semi-natural habitats*", Figs. A1 and A2).

Table 3. Results of the linear mixed models relating spatial community turnover to year (2011 or 2012), proportion of oilseed rape (OSR) and proportion of semi-natural habitats (SNH) within each sampling landscape. Intercepts, model coefficients and the respective standard error of the mean (between brackets) are given. Values not shown (-) were not present in the final model (after backwards stepwise selection). Results for hoverflies during flowering were not available (n.a.) due to their low abundance in this period. All values were transformed (10^4) to improve clarity.

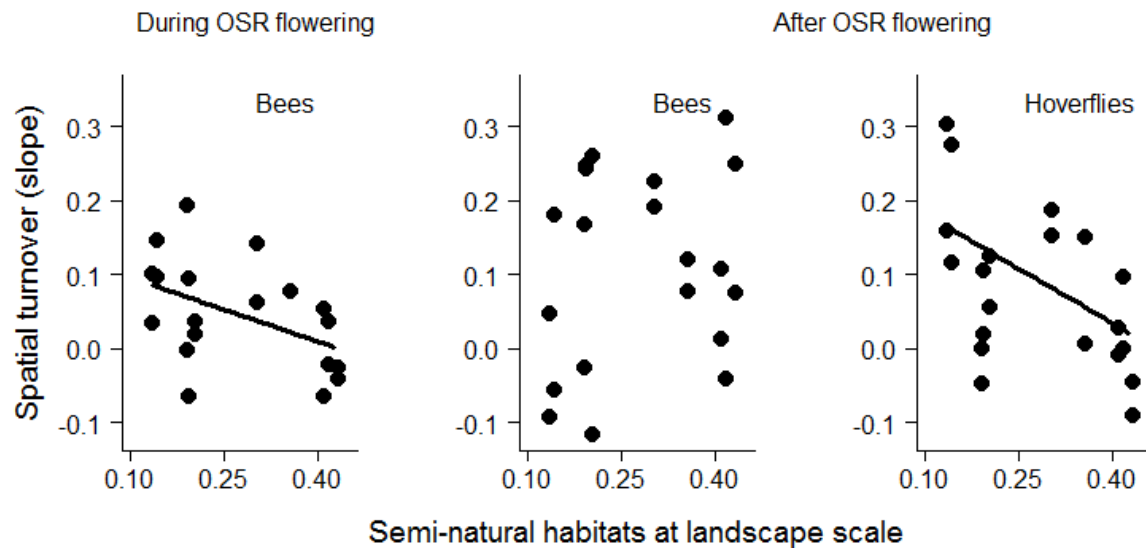| Period	Taxon	Intercept	OSR	SNH	Year
During flowering	Bees	2.21 (0.64)	-	5.2 (2.15)	-
	Hoverflies	n.a.	n.a.	n.a.	n.a.
After flowering	Bees	-	-	-	-
	Hoverflies	2.51 (0.98)	-	-6.84 (3.10)	2.09 (0.62)

Fig 3. Effects of the proportion of semi-natural habitats within landscapes on correlation coefficients for solitary bees (left and center) and hoverflies (right) obtained in linear mixed-effects models. Spatial turnover denotes the Mantel correlation coefficient between a Bray-Curtis dissimilarity matrix for the species at plot level with a dissimilarity matrix based on Euclidean distances between sampling plots (i.e. traps). Higher correlation coefficients represent higher spatial community dissimilarities. Each point depicts one landscape in one year (2011 or 2012). Results are shown for the period during oilseed rape (OSR) flowering (left) and after oilseed rape flowering (center and right).

DISCUSSION

Our results show that the landscape wide proportion of semi-natural habitats can influence spatial community turnover between local assemblages in two key pollinator groups: solitary bees and hoverflies. Even though the proportion of oilseed rape fields did not homogenize community composition, its flowering stage (during vs after blooming) determined the effect of semi-natural habitats on community similarity.

Heterogeneity between local assemblages

Semi-natural habitats had a homogenizing effect on species composition of bees, as they decreased the spatial turnover between sampling points. However, this was only the case during oilseed rape flowering. This pattern can be explained by the strong attractiveness of oilseed rape to pollinators (Holzschuh *et al.* 2011). The great offer of pollen and nectar can be an important resource and bumblebees may disperse large distance to exploit it (Westphal *et al.* 2003). Solitary bees, on the other hand, are strongly constrained by their nesting requirements (Westrich 1996) and disperse only short distances for foraging (Gathmann and Tscharntke 2002; Steffan-Dewenter *et al.* 2002). Nonetheless, solitary bees have been shown to spillover to flowering

oilseed rape fields once the distance was small enough (Holzschuh *et al.* 2011; Kovács-Hostyánszki *et al.* 2013). This indicates that higher proportions of semi-natural habitat could increase the probability of oilseed rape fields within their foraging range, increasing resource availability for solitary bees. The lack of a relevant effect of semi-natural areas after flowering supports this idea, since bees would no longer have a stimulus to spillover to the crop area and community turnover would depend mainly on distance between sampling points and habitat type.

The extremely low abundance of hoverflies during oilseed rape flowering did not allow us to investigate the effect of landscape context on the spatial community dissimilarity in this period. However, previous studies have shown that oilseed rape can also cause landscape-wide dilution of hoverfly populations (Hänke *et al.* 2014), so it is probable that such effect had also occurred here. The low number of hoverflies in May can be connected to their main emergence in late summer in comparison to bees, which are mostly already active in spring (vanVeen 2004, Hänke *et al.* 2014).

In contrary to our expectations, semi-natural habitats strongly affected hoverfly spatial community turnover after oilseed rape flowering. Species richness was higher in crop fields, which is in line with the literature as hoverflies profit from abundant larval prey in arable fields (Meyer *et al.* 2009) and their richness can even increase with distance to semi-natural habitats (Jauker *et al.* 2009). In this sense, increasing proportion of arable area would be expected to show a stronger concentration effect. Nonetheless, even though most hoverfly communities are typically dominated by aphidophagous species (Frank 1999; Hänke *et al.* 2009; Meyer *et al.* 2009), semi-natural habitats may offer more stable resources and may be essential to other guilds, such as xylophagous, phytophagous or coprophagous species (Meyer *et al.* 2009). Additionally, adult hoverflies of all feeding guilds depend on nectar for high-energy flight and pollen for egg maturation (Haslett 1989). Therefore, large semi-natural areas may decrease spatial community turnover in two ways. First, they increase the habitat size and, consequently, the spatial distribution of hoverfly species that depend on these areas for feeding and reproduction. Second, they may also offer flower resources to generalists that spillover from arable fields. The proximity between foraging and oviposition sites could increase the spillover between habitats and decrease spatial turnover of local communities. In fact, although local diversity was lower in semi-natural areas, overall more species were sampled in these habitats than in crop fields. This suggests both a higher number of unique species and a considerable overlap with the other habitats.

The increased spillover of bees and syrphids between semi-natural habitats and arable fields can be unfavorable for native plant species when pollinators are diverted and, as a consequence, seed set is reduced (Holzschuh *et al.* 2011). But mass flowering crops within the foraging range can be advantageous to bees, especially when flowering takes place in early spring, when wild flowers are still rare in semi-natural habitats (Westphal *et al.* 2009; Herrmann *et al.* 2007). Moreover, the spillover of pollinators from arable fields to semi-natural areas, as could be the case for hoverflies, can increase the fitness of native plants, given that high richness of pollinator species increases fruit set (Garibaldi *et al.* 2013). Isolation from semi-natural habitats has been shown to reduce both stability and mean levels of flower-visitor richness, visitation rates and fruit-set in crop areas (Garibaldi *et al.* 2011). Likewise, decreases in evenness and dependence on few species for pollination can be especially detrimental to stability in seed yield (Bommarco *et al.* 2012). Generally, movements of species between habitats in a landscape can be positive, enabling them to perform functions across space and time and possibly guaranteeing resilience (Sristava and Vellend 2005; Tscharntke *et al.* 2012). This capacity to recover functions after disturbance is especially important in agricultural areas, which are characterized by regular changes due to harvest and crop rotation (Wissinger 1997).

Species richness

The higher species richness of bees and hoverflies observed in arable fields other than oilseed rape may be counter intuitive, but concurs with other studies that found higher local diversity of butterflies (DeVries et al. 1997; DeVries and Walla 1999) and bees and wasps (Klein et al. 2002; Tylianakis et al. 2005) in more disturbed areas when compared to semi-natural habitats. In accordance to Tylianakis et al. (2005), this pattern did not always translate into an overall (i.e. all sampling rounds pooled) higher landscape-wide diversity in such habitat types. This could be a consequence of the diversity of crop types or of different management approaches among fields. These results reinforce the idea that managed land cannot be seen as a barren matrix, deprived of biodiversity. Extensively managed crop fields (Kovács-Hostyánszki et al. 2011) and field margins (Meek et al. 2002) may enable high species richness at local and landscape scale.

CONCLUSIONS

Several studies have shown that agricultural intensification can promote homogenization of local communities (e.g. Flohre et al. 2011; Dormann et al. 2007; Hendrickx et al. 2007; Ekroos et al. 2010). However, these studies usually take into account only species composition

per habitat type and do not consider differences in the distribution of species throughout the landscape, characterized by many habitat types. Our spatially explicit approach allowed us to demonstrate that semi-natural habitats can greatly contribute to enhance distance-induced similarity between communities, at least temporarily. It is well known that sites close to each other tend to be more similar (Fortin and Dale 2005). However, community dissimilarity between distant points can be reduced through increased dispersal of individuals (Stephens and Wiens 2004). Larger proportions of semi-natural habitats could foster movements throughout the landscape, thereby generating the observed community homogenization. Such exchanges of individuals between habitats can be important to stabilize pollination services over time, buffering against declines in any individual species, and, consequently, increase the predictability of ecosystem services such as crop yield. Moreover, increasing percentages of semi-natural habitats should promote community resilience after disturbances coming from agricultural management.

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APPENDIX

Table A1. Bee species list and abundance per habitat type. SNH= semi-natural habitats. OSR= oilseed rape fields. Other= other crop fields.

Family	Genus	Species	Author	SNH	OSR	Other
Andrenidae	*Andrena*	*agilissima*	(Scopoli, 1770)	1	1	0
Andrenidae	*Andrena*	*angustior*	(Kirby, 1802)	7	0	7
Andrenidae	*Andrena*	*apicata*	Smith, 1847	0	0	1
Andrenidae	*Andrena*	*bicolor*	Fabricius, 1775	13	1	5
Andrenidae	*Andrena*	*carantonica*	Pérez, 1902	5	1	8
Andrenidae	*Andrena*	*chrysosceles*	(Kirby, 1802)	7	3	14
Andrenidae	*Andrena*	*cineraria*	(Linnaeus, 1758)	4	3	3
Andrenidae	*Andrena*	*combinata*	(Christ, 1791)	0	1	0
Andrenidae	*Andrena*	*congruens*	Schmiedeknecht, 1884	0	0	1
Andrenidae	*Andrena*	*dorsata*	(Kirby, 1802)	0	0	2
Andrenidae	*Andrena*	*falsifica*	Perkins, 1915	2	0	2
Andrenidae	*Andrena*	*flavipes*	Panzer, 1799	26	27	96
Andrenidae	*Andrena*	*florea*	Fabricius, 1793	1	0	0
Andrenidae	*Andrena*	*fucata*	Smith, 1847	7	1	8
Andrenidae	*Andrena*	*fulva*	(Müller, 1766)	8	5	9
Andrenidae	*Andrena*	*fulvago*	(Christ, 1791)	2	0	3
Andrenidae	*Andrena*	*gravida*	Imhoff, 1832	0	1	1
Andrenidae	*Andrena*	*haemorrhoa*	(Fabricius, 1781)	17	17	43
Andrenidae	*Andrena*	*helvola*	(Linnaeus, 1758)	16	1	18
Andrenidae	*Andrena*	*humilis*	Imhoff, 1832	2	0	1
Andrenidae	*Andrena*	*labialis*	(Kirby, 1802)	1	0	1
Andrenidae	*Andrena*	*labiata*	Fabricius, 1781	0	0	1
Andrenidae	*Andrena*	*lapponica*	Zetterstedt, 1838	2	0	1
Andrenidae	*Andrena*	*minutula*	(Kirby, 1802)	16	2	6
Andrenidae	*Andrena*	*minutuloides*	Perkins, 1914	3	0	2
Andrenidae	*Andrena*	*mitis*	Schmiedeknecht, 1883	1	0	1
Andrenidae	*Andrena*	*nigroaenea*	(Kirby, 1802)	136	87	347
Andrenidae	*Andrena*	*nitida*	(Müller, 1776)	14	3	17
Andrenidae	*Andrena*	*praecox*	(Scopoli, 1763)	1	0	1
Andrenidae	*Andrena*	*proxima*	(Kirby, 1802)	4	0	1
Andrenidae	*Andrena*	*semilaevis*	Pérez, 1903	0	0	1
Andrenidae	*Andrena*	*strohmella*	Stoeckhert, 1928	2	0	5
Andrenidae	*Andrena*	*subopaca*	Nylander, 1848	7	1	5
Andrenidae	*Andrena*	*susterai cf.*	Alfken, 1914	1	0	0
Andrenidae	*Andrena*	*synadelpha*	Perkins, 1914	0	0	1
Andrenidae	*Andrena*	*vaga*	Panzer, 1799	2	1	2
Andrenidae	*Andrena*	*varians*	(Kirby, 1802)	13	7	14
Andrenidae	*Andrena*	*ventralis*	Imhoff, 1832	1	0	0
Andrenidae	*Andrena*	*wilkella*	(Kirby, 1802)	2	0	0
Apidae	*Eucera*	*nigrescens*	Pérez 1879	0	0	1

Colletidae	*Hylaeus*	*angustatus*	(Schenck, 1861)	2	0	1
Colletidae	*Hylaeus*	*annularis*	(Kirby, 1802)	8	0	6
Colletidae	*Hylaeus*	*communis*	Nylander, 1852	15	0	4
Colletidae	*Hylaeus*	*confusus*	Nylander, 1853	23	0	4
Colletidae	*Hylaeus*	*gredleri*	Förster, 1871	3	0	0
Colletidae	*Hylaeus*	*hyalinatus*	Smith, 1842	1	0	1
Colletidae	*Hylaeus*	*leptocephalus*	(Morawitz, 1870)	1	0	0
Colletidae	*Hylaeus*	*punctatus*	(Brullé, 1832)	1	0	0
Colletidae	*Hylaeus*	*styriacus*	Förster, 1871	2	0	0
Halictidae	*Halictus*	*confusus*	Smith, 1853	0	1	1
Halictidae	*Halictus*	*rubicundus*	(Christ, 1791)	0	1	9
Halictidae	*Halictus*	*scabiosae*	(Rossi, 1790)	0	1	0
Halictidae	*Halictus*	*simplex*	Blüthgen, 1923	1	1	0
Halictidae	*Halictus*	*tumulorum*	(Linnaeus, 1758)	73	7	55
Halictidae	*Halictus*	*quadricinctus*	(Fabricius, 1776)	0	0	1
Halictidae	*Halictus*	*sexcinctus*	(Fabricius, 1775)	2	0	1
Halictidae	*Lasioglossum*	*calceatum*	(Scopoli, 1763)	25	27	99
Halictidae	*Lasioglossum*	*fratellum*	(Pérez, 1903)	1	0	0
Halictidae	*Lasioglossum*	*fulvicorne*	(Kirby, 1802)	8	7	15
Halictidae	*Lasioglossum*	*laticeps*	(Schenck, 1868)	24	5	54
Halictidae	*Lasioglossum*	*lativentre*	(Schenck, 1853)	3	1	1
Halictidae	*Lasioglossum*	*leucopus*	(Kirby, 1802)	2	2	5
Halictidae	*Lasioglossum*	*leucozonium*	(Schrank, 1781)	12	3	5
Halictidae	*Lasioglossum*	*lineare*	(Schenck, 1868)	0	0	1
Halictidae	*Lasioglossum*	*malachurum*	(Kirby, 1802)	4	4	11
Halictidae	*Lasioglossum*	*minutulum*	(Schenck, 1853)	0	0	1
Halictidae	*Lasioglossum*	*morio*	(Fabricius, 1793)	159	16	242
Halictidae	*Lasioglossum*	*parvulum*	(Schenck, 1853)	0	0	5
Halictidae	*Lasioglossum*	*pauxillum*	(Schenck, 1853)	801	270	1797
Halictidae	*Lasioglossum*	*punctatissimum*	(Schenck, 1853)	0	1	1
Halictidae	*Lasioglossum*	*pygmaeum*	(Schenck, 1853)	1	0	1
Halictidae	*Lasioglossum*	*villosulum*	(Kirby, 1802)	21	1	11
Halictidae	*Lasioglossum*	*xanthopus*	(Kirby, 1802)	2	1	8
Halictidae	*Lasioglossum*	*albipes*	(Fabricius, 1781)	1	0	1
Halictidae	*Lasioglossum*	*rufitarse*	(Zetterstedt, 1838)	4	0	1
Megachilidae	*Anthidium*	*byssinum*	(Panzer, 1798)	1	0	0
Megachilidae	*Megachile*	*centuncularis*	(Linnaeus, 1758)	2	0	1
Megachilidae	*Megachile*	*lagopoda*	(Linnaeus, 1761)	1	0	0
Megachilidae	*Megachile*	*versicolor*	Smith, 1844	0	0	1
Megachilidae	*Megachile*	*willughbiella*	(Kirby, 1802)	0	0	1
Megachilidae	*Osmia*	*aurulenta*	(Panzer, 1799)	1	0	0
Megachilidae	*Osmia*	*bicolor*	(Schrank, 1781)	70	8	51
Megachilidae	*Osmia*	*brevicornis*	(Fabricius, 1798)	1	0	0
Megachilidae	*Osmia*	*caerulescens*	(Linnaeus, 1758)	1	0	0
Megachilidae	*Osmia*	*campanularum*	(Kirby, 1802)	3	0	0
Megachilidae	*Osmia*	*florisomnis*	(Linnaeus, 1758)	14	0	2

Megachilidae	*Osmia*	*leaiana*	(Kirby, 1802)	5	1	0
Megachilidae	*Osmia*	*claviventris*	Thomson, 1872	2	0	0
Megachilidae	*Osmia*	*rapunculi*	(Lepeletier, 1841)	2	0	0
Megachilidae	*Osmia*	*bicornis*	(Linnaeus, 1758)	21	4	8
Megachilidae	*Osmia*	*spinulosa*	(Kirby, 1802)	4	0	0
Megachilidae	*Osmia*	*truncorum*	(Linnaeus, 1758)	0	0	1
Melittidae	*Macropis*	*fulvipes*	(Fabricius, 1804)	1	0	0

Table A2. Hoverfly (Syrphidae) species list and abundance per habitat type. SNH= semi-natural habitats. OSR= oilseed rape fields. Other= other crop fields.

Genus	Species	Author	SNH	OSR	Other
Brachypalpoides	*lentus*	(Meigen, 1822)	1	0	0
Brachypalpus	*valgus*	(Panzer, 1798)	1	0	0
Cheilosia	*sp*		2	0	1
Cheilosia	*albitarsis*	(Meigen, 1822)	7	0	0
Cheilosia	*bergenstammi*	Becker, 1894	1	0	0
Cheilosia	*flavipes*	(Panzer, 1798)	1	0	0
Cheilosia	*pagana*	(Meigen, 1822)	1	0	0
Cheilosia	*ranunculi*	Doczkal, 2000	5	0	3
Cheilosia	*vernalis*	(Fallen, 1817)	2	2	5
Chrysotoxum	*bicinctum*	(Linnaeus ,1758)	5	1	2
Chrysotoxum	*verralli*	Collin, 1940	2	1	1
Dasysyrphus	*albostriatus*	(Fallen, 1817)	1	0	0
Dasysyrphus	*lenensis*	Bagatshanova, 1980	1	0	0
Dasysyrphus	*venustus*	(Meigen, 1822)	2	0	0
Episyrphus	*balteatus*	(DeGeer, 1776)	249	215	1003
Eristalis	*arbustorum*	(Linnaeus, 1758)	0	5	1
Eristalis	*nemorum*	(Linnaeus, 1758)	1	5	4
Eristalis	*tenax*	(Linnaeus, 1758)	1	14	7
Eumerus	*amoenus*	Loew, 1848	0	0	1
Eumerus	*ornatus*	Meigen, 1822	2	0	0
Eumerus	*strigatus*	(Fallen, 1817)	0	0	1
Eupeodes	*sp*		0	1	0
Eupeodes	*corollae*	(Fabricius, 1794)	63	112	378
Eupeodes	*lapponicus*	(Zetterstedt, 1838)	3	1	7
Eupeodes	*latifasciatus*	(Macquart, 1829)	0	0	2
Eupeodes	*luniger*	(Meigen, 1822)	1	0	4
Ferdinandea	*cuprea*	(Scopoli, 1763)	1	0	0
Helophilus	*hybridus*	Loew, 1846	0	0	1
Helophilus	*pendulus*	(Linnaeus ,1758)	0	1	0
Helophilus	*trivittatus*	(Fabricius, 1805)	0	0	2
Heringia	*sp*		0	1	1
Lejogaster	*metallina*	(Fabricius, 1781)	0	0	1
Melanogaster	*nuda*	(Macquart, 1829)	0	1	2
Melanostoma	*mellinum*	(Linnaeus ,1758)	23	14	68
Melanostoma	*scalare*	(Fabricius, 1794)	0	0	3
Meliscaeva	*auricollis*	(Meigen, 1822)	4	0	0
Merodon	*equestris*	(Fabricius, 1794)	2	1	1
Myathropa	*florea*	(Linnaeus ,1758)	3	1	0
Neoascia	*meticulosa*	(Scopoli, 1763)	1	0	0
Neoascia	*obliqua*	Coe, 1940	0	0	1
Neoascia	*podagrica*	(Fabricius, 1775)	1	0	4
Parasyrphus	*annulatus*	(Zetterstedt, 1838)	2	0	0

Pipiza	*quadrimaculata*	(Panzer, 1804)	3	0	0
Pipizella	*sp*		4	0	3
Pipizella	*viduata*	(Linnaeus ,1758)	54	1	17
Pipizella	*virens*	(Fabricius, 1805)	1	0	0
Platycheirus	*sp*		0	0	2
Platycheirus	*albimanus*	(Fabricius, 1781)	15	0	10
Platycheirus	*peltatus*	(Meigen, 1822)	0	1	1
Rhingia	*campestris*	Meigen, 1822	3	4	0
Scaeva	*dignota*	(Rondani, 1857)	19	22	36
Scaeva	*pyrastri*	(Linnaeus ,1758)	3	20	29
Scaeva	*selenitica*	(Meigen, 1822)	10	6	24
Sphaerophoria	*sp*		24	10	86
Sphaerophoria	*interrupta group*	(Fabricius, 1805)	0	0	2
Sphaerophoria	*scripta*	(Linnaeus ,1758)	14	22	84
Syritta	*pipiens*	(Linnaeus ,1758)	0	0	3
Syrphus	*ribesii*	(Linnaeus ,1758)	14	17	17
Syrphus	*torvus*	Osten-Sacken, 1875	82	91	117
Syrphus	*vitripennis*	Meigen, 1822	116	57	161
Temnostoma	*bombylans*	(Fabricius, 1805)	0	0	1
Trichopsomyia	*joratensis*	Goeldlin, 1997	1	0	0
Tropidia	*scita*	(Harris, 1780)	2	0	2
Xanthogramma	*pedissequum*	(Harris, 1776)	0	0	3
Xylota	*segnis*	(Linnaeus ,1758)	11	1	23

SUPPLEMENTARY MATERIAL

Gradients of landscape composition

Table A3. Proportion of area covered by semi-natural habitats (meadows, pastures and forest margins; SNH) and oilseed rape fields (OSR). Minimum, maximum and mean values are shown. Values of OSR are given for 2011 and 2012. Semi-natural areas remained constant in both study years.

Habitat	Minimum	Maximum	Mean
SNH	0.13	0.43	0.27
OSR (2011)	0	0.67	0.21
OSR (2012)	0	0.34	0.16

Effect of number of samples in semi-natural habitats

We tested whether the effect of semi-natural habitats on homogeneity between communities was only a sampling effect, i.e. if it was only resulting of the same habitat type being sampled more often in areas with larger proportions of semi-natural habitats. This was done by limiting the number of samples from semi-natural habitats to five per site (Fig A1). In one year, two out of 10 sites only had four samples collected in semi-natural habitats, given that one pan trap per site was damaged.
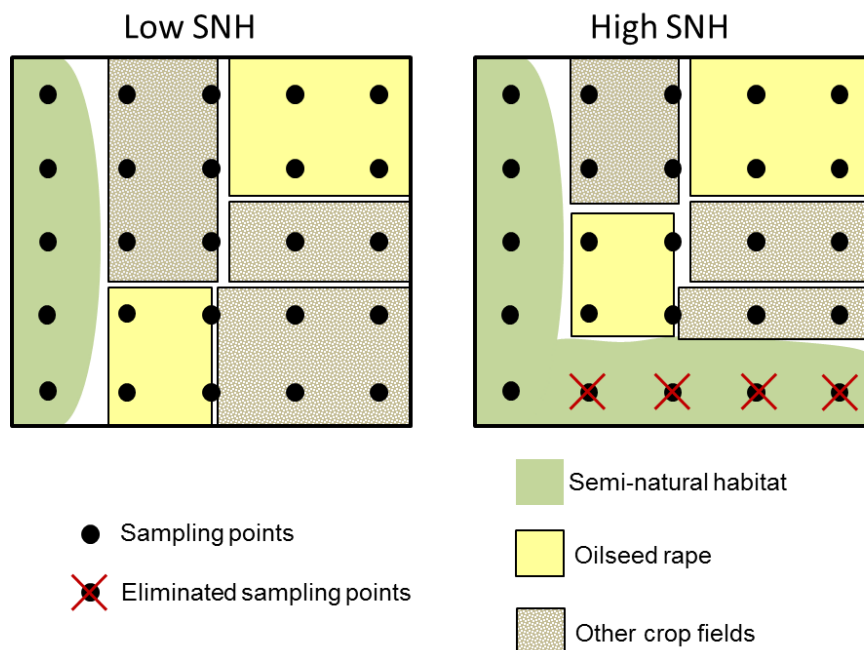

Fig A1. Examples of how the number of samples from semi-natural habitats per site was standardized. Each plot is represented by one sampling point.

The results described in the article did not change substantially (Fig A2). This means that the inclusion of proportion of semi-natural habitats as an explanatory variable decreased AICc values in both bees and hoverflies models. Proportion of oilseed rape fields was not related to the response variables.
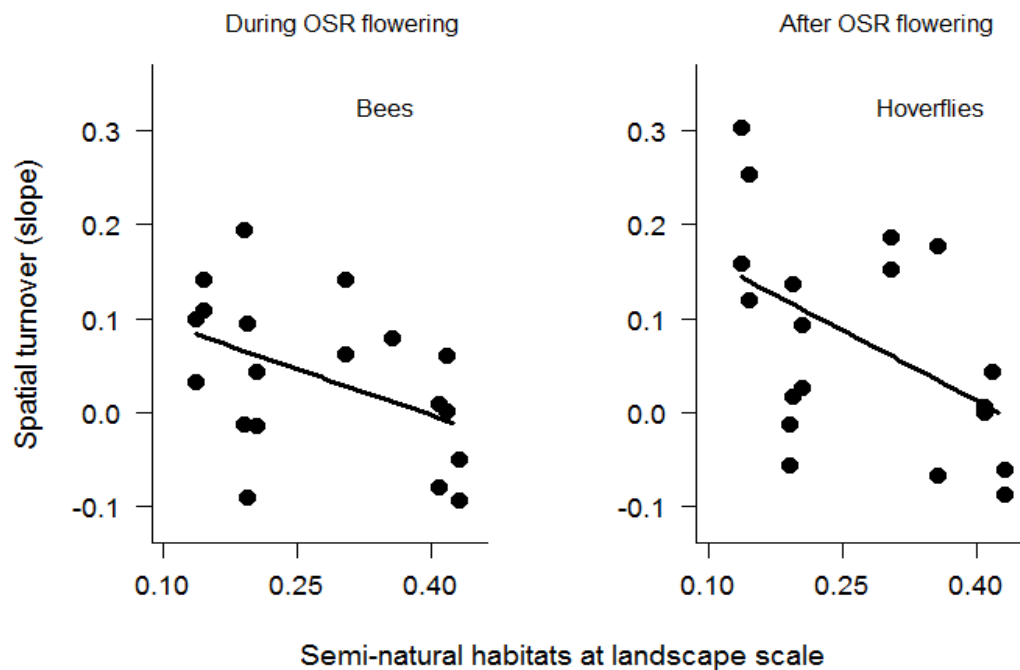

Fig A2. Effects of the proportion of semi-natural habitats within landscapes on correlation coefficients for solitary bees (during flowering) and hoverflies (after flowering), obtained in linear mixed-effects models. Spatial turnover denotes the Mantel correlation coefficient between a Bray-Curtis dissimilarity matrix for the species at plot level with a dissimilarity matrix based on Euclidean distances between sampling plots (i.e. traps). Each point represents one landscape in one year (2011 or 2012).

CHAPTER 5

Synthesis

CONCLUSIONS

The first study demonstrated that sampling design can affect the predictability of landscape-wide biodiversity estimates. Our results showed that number of samples per study area affected the precision of parameter estimation and that sampling only one habitat type generated biased estimates of parameter and species richness. These results show that, when organisms that use resources at landscape scale are sampled only at local scales, the obtained estimates will probably not represent the response of the whole community to the landscape context.

The second study revealed the existence of interannual carry-over effects of landscape composition on pollen beetle and parasitoid abundance. The proportion of oilseed rape in 2010 indirectly affected the abundance of pollen beetles in 2012. This effect was mediated by changes in parasitism rates, which then affected the abundance of newly emerged pollen beetles. Moreover, the effect of oilseed rape area on pollen beetle changed with time. It was negative during oilseed rape flowering, when the population was mainly composed by overwintered beetles, and positive after flowering, when newly emerged beetles were the majority. Our analyses showed that parasitoid-host interactions and the host's population dynamics can be much more complex in the annually changing cropland landscapes than usually thought.

The third study determined that larger proportion of semi-natural habitats promote the homogenization of insect communities. This effect was observed for bees during oilseed rape flowering and for hoverflies after flowering. The proportion of this mass flowering crop had no effect. This decrease in dissimilarity between local assemblages was a consequence of increased exchange of individuals between habitat types. Larger proportions of semi-natural habitats could foster movements throughout the landscape, thereby generating the observed community homogenization. Such exchanges of individuals between habitats can be important to stabilize pollination services over time and promote community resilience after disturbances coming from agricultural management.

In summary, the different habitat types that compose heterogeneous agricultural mosaic landscapes can play different roles for trophic interactions and the structure of insect communities. Larger proportions of semi-natural habitats may increase stability of pollination and biological control by benefiting solitary bees, hoverflies and parasitoids. Mass flowering crops can influence insect communities and population densities, affecting ecosystem services both positively and negatively. This effect may be temporary, limited by the flowering period, or

may extend to the following years, particularly for specialized insects, such as the pollen beetle and its parasitoids. This diversity of effects from different landscape components can be best investigated when all habitat types are sampled. Results originating from only one habitat type cannot be extrapolated to the whole landscape.

In conclusion, landscape planning should take into consideration the movement of organisms between habitat types and through time in order to guarantee conservation of ecosystem services and crop yield. This can only be done if ecological studies also widen their scope in space and time, to account for the dispersal of organisms and the different life cycle stages.

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