



## Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists



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### ABSTRACT

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

In a highly replicated study, we established nesting resources on 95 grasslands in three geographic regions across Germany and measured species richness and abundance of hosts (bees and wasps) and their antagonists, and rates of parasitism. For each site, we quantified local land-use intensity as well as landscape heterogeneity in terms of composition and configuration at spatial scales ranging from 250 m to 2000 m.

Increasing landscape heterogeneity enhanced species richness, abundance and parasitism rate, whereas local land-use intensity only marginally negatively affected total abundance. Bee and wasp abundance as well as wasp species richness were enhanced by landscape composition at 250 m, whereas their antagonists were enhanced by landscape configuration at 1500 m.

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

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## 1. Introduction

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

Moreover, different components of landscape heterogeneity, such as the composition and configuration of landscape, are expected to have distinct effects on different functional groups or ecosystem processes, but this remains largely unexplored (Fahrig et al., 2011; Holzschuh et al., 2010; Kennedy et al., 2013). While composition reflects the number and proportions of different habitat types in a landscape, configuration refers to the spatial arrangement of habitats and their shapes (Fahrig et al., 2011; Li and Reynolds, 1995). Bee abundance and species richness for instance, is enhanced by landscape composition (percentage of non-crop habitats), whereas wasps benefit from high edge density, i.e. landscape configuration (Holzschuh et al., 2010). Still, the role of landscape composition versus configuration for species richness and biotic interactions at different trophic levels remains unclear. Furthermore, species may respond to landscape heterogeneity at

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different spatial scales depending on species-specific dispersal and foraging distances (Steffan-Dewenter, 2002). For example body size (Greenleaf et al., 2007; Westphal et al., 2006), trophic level (Thies et al., 2005, 2003) and resource or habitat specialisation (Tschamtkke et al., 2005) may determine scale-dependent responses to landscape heterogeneity. Moreover, specialists of higher trophic levels are assumed to be more vulnerable to habitat fragmentation and reduced landscape heterogeneity than their hosts (Brueckmann et al., 2011; Chaplin-Kramer et al., 2011; Holt et al., 1999; Rand et al., 2012). Antagonists also have more complex requirements because they have to synchronise their activities in space and time with host abundance (Durrer and Schmid-Hempel, 1995; Steffan-Dewenter, 2003). Structurally diverse landscapes with high connectivity between habitats could improve the chances of finding habitats with host populations, thereby particularly benefiting higher trophic levels. Semi-natural habitats may offer overwintering sites or host species for natural enemies in adjacent crop fields (Rand et al., 2006) and thus serve as refuge habitats in agricultural landscapes. Calcareous grasslands are notably one of the most species-rich habitats in Central Europe (Poschlod and WallisDeVries, 2002; van Swaay, 2002). Here, we chose grassland habitats of different land-use intensities to study land-use effects on arthropods. The management of grasslands determines vegetation structure and richness and thus the availability of resources for arthropod communities (Borer et al., 2012; Socher et al., 2012). Generally, there is a lack of studies dealing with insect diversity and biotic interactions in grassland habitats (Tschamtkke et al., 2012) although grassland habitats account for 29% of the farmed area in Germany (<http://www.bmelv-statistik.de>) and 40.5% of the terrestrial area of the world (<http://www.fao.org>).

We used cavity-nesting bees, wasps and their antagonists in trap nests as a model system to study the responses of different functional groups to local grassland management intensity and landscape heterogeneity. Trap-nesting arthropod species can serve as biodiversity indicator taxa and provide exceptional insights into multitrophic biotic interactions (Steffan-Dewenter and Schiele, 2008; Tschamtkke et al., 1998; Westphal et al., 2008). Hosts in this system are solitary bees, serving as pollinators of wild plants and insect-pollinated crops and predatory wasps that fulfil a crucial role as predators of pest insects (Klein et al., 2004). These host species depend on different habitat types within their foraging range for food supply and nest building (Westrich, 1996).

Due to logistic constraints landscape-scale studies are often conducted in only one study region. However, to allow more general conclusions about impacts of different factors of landscape heterogeneity on functional biodiversity, a replication of studies in several regions is desirable (Fährig et al., 2011; Holzschuh et al., 2007). Here, we present results from a well replicated study conducted in 95 study plots in three distinct regions in Germany (Fischer et al., 2010, <http://www.biodiversity-exploratories.de>) covering three spatial levels in our study: (1) local level of study plots, (2) landscape level represented by eight spatial scales (250 m up to 2000 m radius around study plots), and (3) regional level (represented by three geographic regions across Germany). Within the framework of our study the following questions were addressed: (1) What is the relative importance of local land-use intensity versus landscape heterogeneity for bees, wasps and their antagonists? and (2) Are there different responses of hosts (bees and wasps) and their antagonists to landscape composition and configuration and are these responses scale-specific? Related to these questions, we tested the following hypotheses:

- i. Species richness and abundance of hosts (bees and wasps) and their antagonists are negatively correlated with local land-use intensity.
- ii. Bees, wasps and their antagonists are enhanced by increasing landscape heterogeneity.
- iii. Bees and wasps are more strongly affected by landscape composition and antagonists by landscape configuration.
- iv. The patterns found are independent from the study region.

## 2. Materials and methods

### 2.1. Study plots

The study was conducted within the framework of the DFG-funded project 'Biodiversity Exploratories' (Fischer et al., 2010). The Exploratories are represented by three research regions in Germany (the Biosphere Reserve Schorfheide-Chorin to the National Park Hainich-Dün to the Biosphere Reserve Schwabische Alb, henceforth referred to as Schorfheide, Hainich and Alb, <http://www.biodiversity-exploratories.de>). We established 3.5 m × 15 m study plots on the study sites of the Exploratories (KML-file A1, Table A2). The study sites of the Exploratories differed in their land-use intensities, ranging from extensively managed calcareous grasslands to intensively used pastures and meadows with high mowing or grazing frequencies or both. The study plots within the study sites were fenced with electric wire when necessary to exclude cattle.

### 2.2. Trap nests

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

Altogether, we quantified nine response variables: (1) the total number of brood cells, hereafter referred to as total abundance, (2) number of brood cells of bees and (3) wasps, (4) number of brood cells of antagonists, (5) total species richness, (6) number of bee species, (7) number of wasp species, (8) number of antagonist species and (9) parasitism rate. Parasitism rate was calculated by dividing the number of brood cells attacked by antagonists per study plot by the total number of brood cells per study plot. Empty nests of multivoltine species were not taken into account for the abundance data. For species richness data, individuals from a study plot that could only be classified to higher taxonomic ranks, like genus or family rank, were only counted as additional species in case there was no other species representing that genus or family from the study plot.

### 2.3. Metrics of local land-use intensity

Local land-use intensity was assessed by annual questionnaires and interviews with land-users and land owners (Fischer et al., 2010). Based on this information, we calculated for each

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