Pollinator guilds respond contrastingly at different scales to landscape parameters of land-use intensity

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Abstract

Land-use intensification is the main factor for the catastrophic decline of insect pollinators. However, land-use intensification includes multiple processes that act across various scales and should affect pollinator guilds differently depending on their ecology. We aimed to reveal how two main pollinator guilds, wild bees (specialists) and hoverflies (generalists), respond to different land-use intensification measures, i.e. arable field cover (AFC), landscape heterogeneity (LH) and functional flower composition of local plant communities as a measure of habitat quality. We sampled wild bees and hoverflies on 22 dry grassland sites within a highly intensified landscape (NE Germany) within three campaigns using pan traps. We estimated AFC and LH on consecutive radii (60-3000m) around the dry grassland sites and estimated the local functional flower composition. Wild bee species richness and abundance was positively affected by LH and negatively by AFC at small scales (140-400m). In contrast, hoverflies were positively affected by AFC and negatively by LH at larger scales (500-3000m), where both landscape parameters were negatively correlated to each other. At small spatial scales, though, LH had a positive effect on hoverflies abundance. Functional flower diversity had no positive effect on pollinators, but conspicuous flowers seem to attract abundance of both guilds. In conclusion, landscape parameters contrarily affect two pollinator guilds at different scales. The correlation of landscape parameters may influence the observed relationships between landscape parameters and pollinators. Hence, effects of land-use intensification seems to be highly landscape-specific.

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Abstract

Land-use intensification is the main factor for the catastrophic decline of insect pollinators. However, landuse intensification includes multiple processes that act across various scales and should affect pollinator guilds differently depending on their ecology. We aimed to reveal how two main pollinator guilds, wild bees (specialists) and hoverflies (generalists), respond to different land-use intensification measures, i.e. arable field cover (AFC), landscape heterogeneity (LH) and functional flower composition of local plant communities as a measure of habitat quality. We sampled wild bees and hoverflies on 22 dry grassland sites within a highly intensified landscape (NE Germany) within three campaigns using pan traps. We estimated AFC and LH on consecutive radii (60-3000m) around the dry grassland sites and estimated the local functional flower composition. Wild bee species richness and abundance was positively affected by LH and negatively by AFC at small scales (140-400m). In contrast, hoverflies were positively affected by AFC and negatively by LH at larger scales (500-3000m), where both landscape parameters were negatively correlated to each other. At small spatial scales, though, LH had a positive effect on hoverflies abundance. Functional flower diversity had no positive effect on pollinators, but conspicuous flowers seem to attract abundance of both guilds. In conclusion, landscape parameters contrarily affect two pollinator guilds at different scales. The correlation of landscape parameters may influence the observed relationships between landscape parameters and pollinators. Hence, effects of land-use intensification seems to be highly landscape-specific.

Keywords

wild bees, hoverflies, syrphids, landscape homogenization, plant functional trait

Introduction

The current decline of insect abundance and diversity alerts ecologists and the broad public worldwide (Hallmann et al. 2017, Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021). In particular, the loss of pollinating insects has the potential to endanger the entire ecosystem functioning at several trophic levels across ecosystems. Approximately 87% of all wild flowering plants depend on animal pollination (Ollerton et al. 2011), therefore insect pollinators are essential for the preservation of plant biodiversity (Fontaine et al. 2005, Biesmeijer et al. 2006) and present an extraordinarily important economic factor worldwide (Gallai et al. 2009).

The intensification of current agricultural practices is considered to be one of the main driver for the loss of pollinator biodiversity and abundances (Sánchez-Bayo and Wyckhuys 2019, Wagner et al. 2021). The response of pollinators to land-use intensification should differ between pollinator guilds, since taxa highly differ in their ecological requirements and functional traits. Wild bees and hoverflies belong to the main pollinator guilds in agricultural landscapes across different habitats (Stanley and Stout 2013, Rader et al. 2020). Wild bees are often considered to be habitat specialists due to their particular nesting site requirements and their stationary foraging behaviour in addition to their specialized resource uptake of nectar (Westrich 1996, Johnson and Steiner 2010). Hoverflies, in contrast, are less specialized in nectar uptake (Van Rijn and Wackers 2016), foraging across a wide range of habitats and on much larger scales compared to wild bees (Bankowska 1980, Power et al. 2016, Klaus et al. 2021). As a result, hoverflies are regarded as generalists, which are less susceptible to land-use intensification than wild bees (Jaucker et al. 2009, Blaauw and Isaacs 2014, Aguirre-Gutierrez et al. 2015). However, solid empirical evidence is missing (e.g. Jauker et al. 2019) and a recent long-term study reported a catastrophic decline of generalist hoverflies during the past years in Central Europe (Hallmann et al. 2020). Despite recent attempts, our understanding of how wild bees and hoverflies are affected by different measures of land-use intensification is limited, which hampers guidance for conservation measures and forecasting consequences of pollinator losses (Senapathi et al. 2017, Rader et al. 2020).

Land use intensification leads to a higher coverage of arable fields (Maskell et al. 2019). The current management regimes of these arable fields include a high frequency of mechanical disturbance, the application of pesticides and fertilizers. The resulting landscapes barely offer value for pollinating insects as food resources or nesting sites with the exception of short-flowering mass events (Riedinger et al. 2014). As a result, pollinators are restricted to patches of (semi-)natural habitats within the agricultural matrix. Therefore, increasing amount of arable field coverage incorporates a reduction of food supply and habitat loss, which hampers dispersal and (re-)colonization of habitat patches. Consequently, this leads to a decrease of pollinating insects like wild bees (Senapathi et al. 2017). In contrast, some studies reported positive effects of arable field cover on hoverflies in agriculture landscapes (Haenke et al. 2009, Gabriel et al. 2010, Brandt et al. 2017). Though these mechanisms are not fully understood, it can be expected that wild bees negatively and hoverflies positively respond to arable field cover.

Moreover, land use intensification may cause a loss of landscape heterogeneity (Maskell et al. 2019). The reduction of habitat diversity at the landscape scale reduces the number of potential niches and food resources, thus, landscape homogenization decreases species diversity (Fahrig et al. 2011, Senapathi et al. 2017). Although landscape heterogeneity and arable field cover may often negatively related to each other (Tscharntke et al. 2012), high landscape heterogeneity may compensate negative effects of arable field cover (Maskell et al. 2019). However, it remains unclear how the effect of both parameters changes with spatial scale and which is of greater importance for both pollinator guilds (but see Maskell et al. 2019). Hoverflies may suffer more from landscape homogenization, as they disperse across a wider range of habitats compared to wild bees that forage nearby their nests.

Land-use intensification may reduce the habitat quality of pollinators. Direct and indirect soil fertilization decreases overall plant species diversity (Maskell et al. 2010, Borer et al. 2014), often accompanied with a particular loss of forbs in grasslands (Maskell et al. 2010). This decline in plant diversity is also found in the context of land abandonment of unproductive habitats, such as dry grasslands, as a consequence of land-use intensification and the (subsequent) cessation of traditional land use practices (Habel et al. 2013). The decline of plant diversity may have a negative effect on pollinator diversity, since many pollinator species show a strong specialization towards particular flower traits (Fenster et al. 2004, Fontaine et al. 2006, Fornoff et al. 2017). However, rather than the taxonomic diversity of plants per se, the functional diversity of flower traits should positively affect pollinator diversity (Fontaine et al. 2006, Fornoff et al. 2017). Moreover, particular flower traits that attract pollinators in the landscape may increase the local pollinators. So far, detailed analyses of flowering traits on pollinators are missing in the landscape context, which is an essential part of how land-use intensification affects local habitat quality for pollinators. Hereby, functional flower diversity should have a stronger effect on wild bees, because they show a stronger specialization to specific flower traits compared to hoverflies (Johnson and Steiner 2000, Van Rijn and Wackers 2016). Otherwise flower traits related to attractiveness should have a stronger effect on hoverflies that migrate through the landscape.

In this study, we aim to reveal responses of two important pollinator groups to different measures of land use intensification, in order to get a better understanding of the underlying mechanisms of the current pollinator loss and subsequent ecosystem functioning. As a study system, we used isolated dry grassland patches that are embedded in an otherwise intensively used agricultural landscape in NE Germany. We sampled bees and hoverflies at 22 dry grassland patches within three sampling campaigns using pan traps. Further, we quantified the local flowering plant community at the time of sampling and estimated different measures of local flower diversity and 'attractiveness'. We determined arable field cover and landscape heterogeneity on consecutive radii from 60m - 3000m around the dry grassland sites, in order to reveal the 'scale of effect' (Jackson and Fahrig 2015), i.e. the spatial scale at which the predictor has the strongest influence on the response variable.

We hypothesize that

1) the proportion of a able field cover surrounding the dry grassland sites has a negative effect on wild bees (species richness and abundance) and a positive effect on hoverflies,

2) landscape heterogeneity has a stronger positive effect on hoverflies compared to wild bees,

3) the spatial scale at which arable field cover and landscape heterogeneity affect the pollinator guilds, is

smaller for wild bees than for hoverflies,

4) functional flower diversity positively affects wild bees in particular and flower traits that are associated with 'attractiveness' positively affect hoverflies in particular.

Methods

Study area

This study was conducted in the north-eastern part of the federal state of Brandenburg in Germany (AgroS-capeLab, http://www.zalf.de/de/struktur/eip/Seiten/AgroScapeLab.aspx, $52^{\circ}52^{\circ}N - 53^{\circ}23^{\circ}N$, $13^{\circ}20^{\circ}E - 14^{\circ}12^{\circ}E$). The study area is located at the transition zone of the west-European oceanic and the east-European continental climate and is characterized by a temperate climate (8.6°C) with an annual precipitation of 563 mm. The region is sparsely populated and a typical Central European agricultural landscape, to a great extent intensively used for agriculture (~ two thirds of the area, Fig. 1). The dominant crop types are wheat, barley, maize and rape seed. The remaining area is mainly covered by forests and (mostly intensively managed) grassland. Dry grasslands are found mainly on hills and slopes or former military areas and make less than one percentage of the land cover. They are remnants of the former extensive farming system of sheep grazing, and today sheep or cattle grazing and mowing is used to preserve some of the remaining patches. The sampled dry grassland plant communities belong to the class *Festuco-Brometea* with some elements of the class *Koelerio-Corynepheretea*, which developed under the constant land use of humans as pastures for several hundred years. Dry grassland patch sizes vary between $270m^2$ and $100.000m^2$, with a median of $5600m^2$.

Sampling design

At 22 dry grassland sites (Fig. 1), three pan traps (yellow, blue, white; 19,6 x 15,4 cm with a 300ml 8%-Formaldehyde-water-dish wash-solution) were attached to sticks approximately 40cm above the ground in a triangle 1m wide triangle. The traps were installed for three sampling campaigns in 2017: May (15/5-18/5/2017), June (12/6-15/6/2017) and August (15/8-18/8/2017), located at representative sites of the patches. Each trap stayed for 48 hours in the field within each sampling campaign. The weather conditions were sunny and dry throughout sampling campaigns.

Specimens were needled and determined to species level using Amiet et al. (1999-2017) and Scheuchl (2000-2006) and van Veen (2010) and Bot and van de Meutter (2019) for the hoverflies.

Flowering plant sampling

During the three sampling campaigns, we recorded all flowering forb species (henceforth plant species) nearby the pan traps, in order to characterize the local plant community, respectively the nectar supply for the pollinators. For this purpose, we placed a circle (r=5m) around the traps with eight equally sized segments ('pie slices'). For each segment, we recorded the presence of flowering forb species (excluding wind-pollinated forbs Sanguisorba minor and Plantago lanceolata), in order to have a measure of local abundance for the forbs (ranging from zero to eight). In orientation to Fornoff et al. (2017), we gathered functional flower traits of the recorded forbs that are considered to be relevant for pollinators from Biolflor Database (Klotz et al. 2002) and Jäger (2016): UV radiation [a,b], UV reflectance [numeric 1-6], color [categorical: yellow, red, blue, white, rose, purple, violet], flowering height [continuous] and nectar access [categorical: open, half-open, hidden] (Supplementary information, Appendix 1). We hypothesized that functional diversity of these traits positively affect pollinator diversity (hypothesis 4). Further, we predict that a higher share of yellow flowers attract a higher number of pollinators, since this color is preferred by numerous bee and hoverfly species (Leong and Thorpe 1999, Lunau 2014). A larger flowering height is supposed to attract more pollinators, first, because of the generally high conspicuousness of tall floral units, second, because of the "effective pollination" hypothesis, according to which tall stature resulting from strong apical dominance attracts greater pollinator visitation, thus allowing larger pollen loads (Donelly et al. 1998).

Determination of landscape parameter

Both landscape parameters, cover arable fields and landscape heterogeneity, were determined on the basis of the biotope mapping of the federal state Brandenburg (lfu.brandenburg.de/lfu/de/aufgaben/natur/biotopschutz/biotopkartierung/). The map distinguishes a large variety of habitats. However, for this study, we used only the twelve main habitat categories: arable fields (64% cover within the study area), forests (13%), grasslands (11%), swamps (2%), built-up areas (3%), standing waters (3%), anthropogenic immature soils (2%), deciduous copse and avenues of trees (1%), parks and cemeteries (1%), dwarf shrub heaths (<1%), streaming water including shores (<1%) and special biotopes (<1%). For small parts of our study area in the federal state Mecklenburg-Vorpommern. we conducted a biotope mapping by ourselves with the help of aerial images. Arable field cover is defined as the percentage of arable field cover around the traps for a specific radius. Landscape heterogeneity is defined as the Shannon-Diversity of main habitat types weighted by their coverage (Maskell et al. 2019). We calculated both landscape predictors for continuous radii from 60m – 3000m. Cover of arable fields and landscape heterogeneity were shown to have a scale-dependent correlation (Supplementary information, Appendix 2). At small scales (<500m) no significant clear correlation was found, whereas at larger scales (>500m) both measures tended to be negatively related to each other.

Statistical analyses

We analyzed the effect of landscape parameters (arable field cover and landscape heterogeneity) and different measures of the local flowering plant community on wild bee and hoverfly species richness and abundance, i.e. number of caught individuals, of a respective site. Apis mellifera, the European honey bee, was excluded from all analyses. Arable field cover, landscape heterogeneity and plant community attributes were investigated in separate models, but the overall model structure was the same. We used GLMMs with poisson distribution and a log-link function for both response variables species richness and abundance (*qlmer*, R-Package lme4, Bates et al. 2020). As covariates, we included sampling campaign as categorical fixed-effect and study site as random-effect to account for the nested design of the study. About 92% of all hoverfly individuals (n=214) were caught in the third sampling campaign and 3/4 of the sites within the first two campaigns did not contain any hoverflies, which is a typical pattern for agrarian landscapes (Brandt et al. 2017). Due to this highly unequal distribution across the sampling campaigns, we restricted our analyses of of local plant attributes on hoverfly species richness and abundance for the third sampling campaign. For these, we used GLMs with poisson error for species richness and negative binomial for abundance without any covariates, as we had no pseudo-replication in this dataset. We assured that model assumptions (normality and over-/underdispersion of residuals, heteroscedasticity, spatial autocorrelation of response variables and model residuals and zero-inflation) were not violated with R-package DHARMa (Hartig and Lohse 2020).

In order to reveal the effects of arable field cover and landscape heterogeneity on pollinators (hypothesis 1 and 2), we determined the scale of effect, i.e. at which spatial scale a landscape parameter has the largest effect on the response variable (Jackson and Fahrig 2015, hypothesis 3). For this purpose, we used the *multifit* -function of Huais (2018), which compares a series of models that differ solely in the scale a landscape parameter was quantified (see the specific model structure above). In our case, we compared models of arable field cover and landscape heterogeneity that were quantified at radii between 60m and 3000m. Landscape predictors were standardized (z-scaled) for each radius in this analysis that parameter estimates are comparable (Schielzeth 2010). The model with the lowest AIC was considered to be the best model. Further, we assured that the natural distribution of dry grasslands in clusters did not affect our results due to possible pseudoreplication of the landscape parameters (Supplementary information, Appendix 3). Additionally, we assessed whether the predictors had a statistically clear effect *sensu* Dushoff et al. (2019).

We predicted that functional diversity of flowers and traits associated with attractiveness have a positive effect on pollinators (hypothesis 4). Functional diversity was estimated with Rao's quadratic entropy (FD_{trait}) of the different traits (see above) and the 'attractiveness' with community weighted mean (CWM_{trait}) (Fornoff et al. 2017). The frequency that a forb species occurred within the eight segments of the vegetation survey was used as abundance measure for the weighting of forb species. In a first step, we checked for possible correlations between $FD_{trait,}$, CWM_{trait} and number of flowering forb species (Supplementary information, Appendix 4). Due to multiple correlations, we included only parameters that were not strongly related to each other ($|\mathbf{r}| < 0.6$): number of flowering forbs, $FD_{flowering height}$, $FD_{color,}$, $FD_{nectar access}$, $FD_{UV reflectance}$, and CWM traits that should attract pollinators, $CWM_{color yellow}$ (percentage of yellow flowering species) and CWM_{flowering height} in our full model. In order to find the most likely parameter combination of local plant community attributes that explain pollinator richness and abundance, we applied an information theoretic approach and compared all possible submodels derived from the full model with AIC_c (Burnham and Anderson 2002). Since several models performed equally well, we performed model averaging over the best models (delta AIC_c < 6, Harrison et al. 2018), in order to get more reliable parameter estimates (Dormann et al. 2018). Local plant community attributes were not correlated to the landscape predictors at any scale. All analyses were carried out in R Version 4.1.0 (R Core Team 2021).

Results

We caught in total 1419 individuals of 79 wild bee species, excluding *Apis mellifera* (honey bee). Most bee individuals were caught in May (n=611) followed by June (n= 498) and August (n=310). Hoverflies were predominantly (92%) caught in August with 214 individuals of 21 species in total.

We observed 121 flowering animal-pollinated plant species (Table S1, Online Appendix 1). Flowering plant species richness ranged from one to 22 species near the pan traps with the highest number in June (mean \pm SD =11.55 \pm 5.4) followed by August (9.05 \pm 4.75) and May (7.41 \pm 3.45).

We found contrasting effects of arable field cover and landscape heterogeneity on both pollinator guilds (Fig. 2). Arable field cover negatively affected wild bee species richness. This effect was statistically clear (p<0.05) at small to intermediate spatial scales (140-400m) and peaked around 200m. Hence, dry grasslands that feature high proportion of arable fields in the surrounding show on average less wild bee species. In contrast, hoverfly species richness and abundance were positively affected by arable field cover at much larger scales (500-3000m), supporting hypothesis 1.

Landscape heterogeneity positively affected wild bees (Fig. 2, 3). Similar to the effect of arable field cover, the scale of effect for species richness had a peak at intermediate spatial scales (580m). Hoverfly species richness and abundance were negatively affected from intermediate to large spatial scales ($^{500m} - 3000m$). On these scales arable field cover and landescape heterogeneity were negatively related to eachother (Supplementary information, Appendix 2). At small spatial scales (120m), landscape heterogeneity had a statistically clear positive effect on hoverfly abundance, indicating that a heterogeneous environment in the vicinity of dry grasslands increase the abundance of hoverflies. Overall, we found no support that landscape heterogeneity particularly enhance hoverflies compared to wild bees (hypothesis 2). Yet, our scale-crossing analyses showed that wild bees were mostly affected on smaller spatial scale compared to hoverflies (with the exception of the positive effect of landscape heterogeneity on abundance) supporting hypothesis 3.

We predicted that functional flower diversity in particular positively affects wild bees and flower traits associated with 'attractiveness' has a positive effect on hoverflies (hypothesis 4). Species richness of both guilds was not affect by any parameter of the plant community, except a negative effect of FD_{nectar access} on hoverflies (Fig. 4). Abundance of wild bees and hoverflies was positively affected solely by CWM_{flower height}. However, we observed also negative effects of plant community attributes on wild bee abundance (FD_{flower height}, FD_{nectar access}, CWM_{color yellow}) and hoverfly abundance (FD_{nectar access}). In summary, we found no evidence that functional diversity enhance pollinators, but the effect of CWM_{flower height}, indicate that plant communities with conspicious flowers may attract pollinators.

Discussion

The catastrophic decline of pollinators and other insects calls for a thorough understanding of the underlying mechanisms to provide measures for nature conservation and mitigate losses of ecosystem services. In this

study, we showed that two important pollinator guilds of Central Europe responded differently to parameters of land-use intensification and at different spatial scales. Further, our study indicates that functional diversity of flower traits as a measure for habitat quality seems to have no particular positive effect on pollinators, highlighting the role of landscape processes to maintain pollinator diversity.

Arable field cover

Arable field cover had a negative effect on wild bee species richness and abundance supporting previous studies that show negative effects of land use intensification on local pollinator diversity in agricultural landscapes (Senapathi et al. 2017). Hoverflies were, in contrast to wild bees, positively affected by the cover of arable fields, indicating that dry grasslands surrounded by a high share of arable fields, have a higher hoverfly species richness and abundance. Although this positive effect seems counterintuitive at first sight, similar observations were made for agricultural fields and flower strips (Brandt et al. 2017, Haenke et al. 2009, Gabriel et al. 2010). Since hoverflies are highly mobile, they may be attracted by specific habitats, if the landscape offers no food resources (Haenke et al. 2009). As a result, hoverflies may accumulate on dry grasslands with a high proportion of arable field cover. Under this consideration, the observed 'positive' effect of arable field cover on hoverfly diversity indicates simply a limitation (and concentration) of food resources within the whole landscape (Haenke et al. 2009). In summary, our study demonstrates that arable field cover is an important predictor for pollinators that affect both guilds contrastingly not only in agricultural ecosystems (e.g. Brandt et al. 2017), but also in (semi-) natural habitats that present 'biodiversity hotspots' in Central Europe (Habel et al. 2013).

Landscape heterogeneity

Landscape heterogeneity should have a positive effect on pollinators, as heterogeneous landscapes provide more niches with a higher diversity of food resources and nesting sites (Fahrig et al. 2011, Hopfenmüller et al. 2014). We predicted that generalist hoverflies benefit more from landscape heterogeneity compared to wild bees, as they forage across a wider range of habitats (H2). In our study, wild bees were positively affected by landscape heterogeneity at intermediate spatial scales (340-780m). Similar, hoverfly abundance was positively affect at small scales (100-140m). However, at large scales (<750m), landscape heterogeneity had continuously a negative effect on hoverflies. We expect that the observed negative relationship of hoverflies to landscape heterogeneity is primarily driven by hoverfly responses to a limitation of other resources in the landscape (see above), since both landscape heterogeneity and arable field cover are negatively related to each other at large scales. Hence, positive effects of landscape heterogeneity may only be important for hoverflies, if landscape heterogeneity is uncorrelated to arable field cover (as in our study for small spatial scales). In conclusion, we found no support for the hypothesis 2, which may be reasoned by specifics of our landscape, though negative correlations between arable field cover and landscape heterogeneity should be present in many areas worldwide (Tscharntke et al. 2012).

Scale-dependency

We predicted that wild bees are affected on smaller scales compared to hoverflies (H3). Landscape heterogeneity and arable field cover affected wild bees at spatial scales that correspond to maximal foraging distances from the nest of small bees (140m - 350m, Wright et al. 2015). In contrast, hoverflies that 'migrate' through the landscape were affected at much larger spatial scales (>750m, with the exception of the positive effect of landscape heterogeneity on hoverfly abundance, see below). Taking together, these results support our hypothesis and indicate that the scale of effect, i.e. at which spatial scale has a landscape parameter the largest effect on a response variable, depends on the foraging behavior of pollinators. However, we detected other scales of effect than previous studies. For example, Meyer et al. (2009) found the strongest (positive) effect of landscape heterogeneity on hoverfly richness in calcareous grasslands on 250m, while Földesi et al. 2015 observed that landscape heterogeneity positively affected hoverfly species richness at smaller spatial scales (300m) compared to wild bees (500m). These deviations demonstrate that the scale of effect may be primarily driven by the landscape context rather than the ecological traits of the species (Galán-Acedo et al. 2018), making it tricky to deduce the scale of effect for other landscapes. Moreover, our study shows that even the direction of landscape effects may change with spatial scale. As outlined above, we assume that the negative effect of landscape heterogeneity on hoverfly abundance arises due to a negative correlation with arable field cover. Therefore, it seems likely that the scale of effect and even the direction of landscape parameter effects is driven by correlations between landscape parameters that are associated with different processes and change with scale. Therefore, we see a strong need to thoroughly analyze and report correlations of possible confounding landscape predictor across scales, in order to better understand the underlying mechanisms of how the scale of effect and direction of landscape effects arise.

Functional flower traits

The outstanding diversity of morphological and coloration traits in animal-pollinated flowers is one of the most recognized examples for niche differentiation in animal communities in ecology. Hence, functional diversity of flowers is considered to positively affect pollinator diversity and vice versa (e.g. Fontaine et al. 2006, Fornoff et al. 2017). However, we found no evidence that neither functional flower diversity nor species richness of flowering plants positively affected both pollinator guilds. This is indeed surprising, since we investigated a strong gradient from one to 22 flowering plants in our study sites. Similarly, to our study, Fornoff et al. (2017) neither found strong positive effects of functional flower diversity on pollinator species richness in experimental plant communities of the size $1m^2$. These plant communities were set even in the same landscape context and therefore local effects should appear more clearly, compared to our study. Possibly, the flower diversity at a rather small scale (in our case study 10m diameter circle) may play a minor role for pollinator diversity, as they are highly mobile and may search nectar resources over large distances of several hundred meters (see above). A valid estimation of functional flower diversity at such scales is hard to achieve, but may be indicated by the positive effect of landscape heterogeneity on both pollinator guilds in our study (see above). Alternatively, diversity of flower traits is negligible in our system, as species are less specialised on particular flower traits than expected. Only six out of the 80 caught wild bee species are listed as oligolectic in our data set (Westrich 2019). While a previous study within our study area observed a much higher share of oligolectic species (Saure and Berger 2006: 28 out of 161), our pollinator community seems to become less specialized as a consequence of possible fragmentation and land-use intensification (Jauker et al. 2019). Hereby, the observed negative effects of functional flower diversity on pollinator abundance may indicate that particular flower types are not accessible for the present pollinator species, as specialized species disappeared. Under such circumstances, the quantity of few plant species with high floral rewards rather than the diversity of flowers may maintain pollinator diversity (Bergamo et al. 2020), as indicated by the positive effect of $\text{CWM}_{\text{flower height}}$ on pollinator abundance, since large plants produce more flowers and are more attractive for pollinators (Donnelly et al. 1998).

Landscape context and pollinator composition

The specific landscape context may modulate the observed responses of pollinators. Although we are confident that similar findings (and correlations between landscape predictors) can be expected in other regions. we would like to highlight that our study area belongs to the most intensified landscapes in Europe (for comparison: 39 % of the total land area of the EU is cropland, around our study patches mean of 60%) with a long history of intensive fertilization and pesticides input. Therefore, we assume that the past land-use intensification already had a tremendous effect on the species pool in the area and the species composition in our study is only a small subset of the species pool of some decades ago. The comparison with previous studies in our study area (Hahn 2002, Saure and Berger 2006) indicates that on the one hand oligolectic bee species disappeared (see above), but also common hoverflies. We observed remarkably low ratios between hoverflies and wild bee individuals compared to studies of similar study systems (our study 1419 wild bees vs. 214 hoverflies, ratio = 0.15; Mudri-Stojnić et al. 2012: ratio 0.83, Jauker et al. 2009: ratio: 0.82, Jauker et al. 2019: ratio 0.95). In particular, generalist aphidophagous species (e.g. Eupeodes corollae. Sphaerophoria scripta) that occur in high densities (e.g. Hahn 2002 for our landscape, Bankowska 1980), are underrepresented in our study, which concurs with the decline of common hoverfly species (Hallmann et al. 2021). These deviations are most likely a consequence of the high land-use intensity in our study region, which is the main factor for the current insect decline (Wagner et al. 2021) and question the hypothesis that

hoverflies are less vulnearble than wild bees.

Conclusion

In conclusion, we observed contrasting and scale-dependent responses of wild bees and hoverflies to measures of land-use intensification, with no particular effects of local flower diversity of plants. As a consequence, pollination service on dry grasslands should change with the surrounding landscape. In homogeneous landscapes with a high share of arable field cover, insect pollination should occur less frequent, due to lower numbers of wild bee individuals and species. Although hoverflies concentrate particularly in these landscapes at dry grasslands they cannot compensate absence of wild bees, as they are less specialized to particular flower types and appear only in late summer in reasonable amounts (see also Brandt et al. 2017). Moreover, the comparison with historical data indicate that species composition and abundance of both guilds already shrunk in our study area, presumably due to high land-use intensification. In order to achieve a better understanding of how land-use intensification affects pollinators, we advocate to a) acknowledge that landscape effects may differ between landscapes and b) analyze therefore possibly confounding landscape parameters across scales.

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Figure legends

Fig. 1 Overview of the study area and sampling design. a) Most of the study area is used for agriculture fields (grey). Forests (dark green) make up to 13%. Grasslands (light green) are mainly intensified, wet grasslands or fallows. b) For each sampling site the cover of arable fields and landscape heterogeneity was calculated for different radii (60m - 3000m) around the site. c) dry grasslands are found mainly on smaller hills or slopes, often surrounded by arable fields.

Fig. 2 Wild bee (a) and hoverfly (b) responses to arable field cover (black) and landscape heterogeneity (red) across multiple scales (60m-3000m). The graphs show the parameter estimates of the models for both predictors on both response variables species richness (solid line) and abundance (dashed line) for each specific radius. Thick lines refer to models, in which the parameter had a statistical clear (p<0.05) effect on the response variable. The triangles refer to the scale of effect, i.e. the scale at which the landscape predictor has the largest effect (lowest AIC, see Fig. 3).

Fig. 3 Effect of arable field cover (a, b) and landscape heterogeneity (c, d) on wild bee (a, c) and hoverfly (b, d) species richness (SR). The graphs show the relationships at the scale of effect, i.e. the radius at which the landscape parameter has the largest effect on the response variable (compare Fig. 1). The different colors refer to the three sampling campaigns. The dotted lines in the hoverfly plots refer to analyses (GLM) that included only the third sampling campaign.

Fig. 4 Effects of local plant community attributes on wild bees (a) and hoverflies (b). The figure shows parameter estimates and confidence intervals of the averaged models for species richness (black) and abundance (grey). The local plant community was recorded during pollinator samplings within a circle (r=5m) around the traps. Please note that for hoverflies, only the third sampling campaign was analyzed (see Methods). SR= Species richness; FD = Functional diversity; CWM = community weighted mean.

Declarations

Data accessibility – We will store all collected data at the open research database of ZALF (http://open-research-data-zalf.ext.zalf.de/default.aspx), which is a master data repositories of Web of Science. Data will be freely available as soon as the manuscript is published. DOI will be 10.4228/ZALF + Suffix.

Conflict of interest – The authors declare no conflict of interest.

Author contributions – The study was conceived by KB, LW, MR and LS. Experimental design and data collection was carried out by LS and KB. Specimens were determined by LS (wild bees) and MR (hoverflies). KB analyzed the data and worte the first draft of the manuscript. All co-authors discussed the findings and contributed during the writing process.

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