Report on the impact of plant diversity and landscape composition and configuration on competition for floral resources between wild and managed pollinators

Deliverable D2.4

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Safeguard
Safeguarding European wild pollinators

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Summary

Wild bees are declining, and habitat loss and the reduction of habitat quality resulting in the loss of flower and nesting resources are considered the main causes of this decline. Increasing densities of honeybee colonies in many regions have led to growing concerns that competition with honeybees exacerbates the decline in wild bees. However, evidence for competition between bees is still limited and it probably occurs only under certain environmental conditions.

In a review article, we explored the impact of floral resource limitation on interactions between flowers and pollinators, which strongly depends on when, where and in what regions of functional trait space floral resources are limiting. We reviewed existing methods for measuring and analysing floral resource structure and identified opportunities for future methods development. We then discussed the causal relationships linking floral resource structure to pollinator coexistence and how these processes can be influenced by exogenous drivers like climate, land use, and episodic disturbances.

In an empirical study at 16 sites from the field site network in two German regions, we assessed nectar depletion rates – an index of resource limitation and competition – based on a comparison of bagged and unbagged flowers. Overall depletion rates were estimated at 95% and 79% in the two regions, indicating strong nectar limitation and likely competition among pollinators for nectar during summer. In a follow up study, we examined nectar limitation in the same region, but during spring when floral resource levels are expected to be much less limiting. We found generally much lower depletion in our spring study compared to the summer study. In both studies, there was no indication in that site-level variation in nectar depletion was driven by honeybee density.

Across 304 sites of the European field site network, honeybee densities were not negatively related to species richness and densities of solitary bees and bumblebees. Furthermore, there was no significant interaction between honeybee densities and environmental variables related to flower availability at local and landscape scales. Thus, honeybee-wild bee relationships were not modulated by environmental variables. Interestingly, we found a positive relationship between honeybee density and densities of solitary bees and bumblebees, even though flowering plant richness and flower cover were included in the models to control for shared responses of honeybees and wild bees to these flower variables. In the experimental study in Germany, weight gain and gyn production in 80 bumblebee colonies on 20 grasslands did not decline with increasing honeybee densities in the grassland. Thus, we found no indication of honeybee-wild bee competition.

Our data suggest a strong overlap in resource use between honeybees and wild bees but do not provide evidence for competition. Although nectar availability was strongly limited during summer (but not during spring) in German grasslands, bumblebee fitness was not affected by honeybee densities. We conclude from our study that reducing honeybee densities in and around valuable wild bee habitats (e.g. by reducing the number of honeybee colonies or by banning honeybee colonies from a buffer around valuable bee habitats) is a justified measure from a precaution perspective, but with low chance to enhance wild bee density and richness in these habitats. Instead, we urgently need conservation measures that improve local habitat quality by enhancing flowering plant species richness and nesting sites. Besides, improving the quality of agricultural landscapes should have the highest priority: Agricultural landscapes with small field sizes and a high proportion of organic farming benefit wild bees in Natura 2000 and other highly protected bee habitats that are imbedded in these landscapes and should also support honeybees with additional resources while reducing shortage of pollen and nectar for potential inferior wild bee species.

List of abbreviations

bft	**Beaufort scale**
EU	**European Union**
GLMM	**generalized linear mixed models**
min	**minutes**
SE	**standard error**

1. Introduction

Wild bees are declining and one of the main reasons is a decline of flower resources, which can result e.g., from abandonment of extensive grassland management at the local scale or the increase of intensive agriculture in the surrounding landscape. Also honeybees which are managed for honey production and for their pollination services in agriculture, depend on wild flower resources. Flowering crop fields usually do not provide food resources constantly throughout the season. This forces honeybees – like wild bees – to forage in semi-natural habitats (Danner et al. 2016). Thus, honeybees also visit flowers in protected habitats located within their foraging range, where they meet wild pollinators relying on these habitats. Furthermore, beekeepers specifically place honeybee colonies in the vicinity of protected habitats with the expectation that their honeybees benefit from a high flower availability there. This has led to increasing concerns that honeybees compete with wild bees for nectar and pollen resources in protected habitats (González-Varo & Vila 2017), and that honeybees intensify the flower scarcity and contribute to the decline of wild bees (Magrach et al. 2017, Mallinger et al. 2017, Thomson & Page 2020, Wojcik et al. 2018).

However, it is unclear how common negative relationships between densities of honeybee and wild bees are, and whether competition with honeybees is one of the causes of the decline of wild bees. Evidence for competition between bees is still limited and it probably occurs only under certain environmental conditions. Obviously, it depends on the amount of flower resources and is only expected where flower resources are limited. Multiple factors such as the diversity of floral resources and the exploiting pollinator community, flowering plant and pollinator traits, foraging strategies, and spatial as well as temporal variation of these factors determine the occurrence of competitive situations. However, a theory-driven conceptional framework under which conditions floral resources and interacting pollinator communities face competitive conditions has currently been lacking. Further, methods that allow a direct quantification of not only potential resource availability indicated by the richness and cover of flowering plants, but also direct measures of resource depletion rates are currently not well developed.

As part of this deliverable, we (1) developed and published a novel framework for "**Pollinator competition and the structure of floral resources**" (Sponsler et al. 2023) and (2) established and tested novel methods to quantify actual resource depletion rates in different seasons. We find that "**High rates of nectar depletion in summer grasslands indicate competitive conditions for pollinators**" (Sponsler et al. 2024a) whereas lower nectar depletion rates in spring resource pulses give less indication for pollinator competition (Sponsler et al. 2024b: "**Pollinator competition and the contingency of nectar depletion during an early spring resource pulse**"). **The findings of these publications are summarised in the abstract of the deliverable and the publications are attached in the Appendix.**

The focus of the presented work is on unpublished results from the Safeguard European field site network, where we collected data on honeybee and other bee pollinator richness and densities, floral resource richness and cover and landscape composition as indirect measures of resource availability. Based on current understanding of floral resource competition, we expect that the negative relationship between honeybee and wild bee densities will be strongest if flower availability is low, honeybee densities are high, resource use of honeybees and other pollinators is overlapping, and honeybees are more efficient in the exploitation of available resources due to intra-colony communication (Nürnberger et al. 2017). Honeybee densities strongly vary locally and across Europe with much higher colony densities in southern Europe compared to central and northern Europe (Breeze et al. 2014), Currently, evidence for these assumptions is mixed (Thomson & Page 2023) and large-scale systematic data across Europe are lacking. We used data from 304 sites of the Safeguard European field site network to assess how common negative relationships between densities of honeybee and wild bees are. To test the modulating effect of flower availability, we assessed the interaction of honeybee densities with flower cover, the species richness of flowering plants and with habitat area at the local scale, and with seminatural habitat amount and cropland cover at the landscape scale.

Bumblebees are particularly prone to competition with honeybees because of a wide overlap in the use of floral resources (Franco et al. 2009; Weaver et al. 2022). A niche overlap of up to 80-90% suggest that honeybees and bumblebees interact while they forage (Thomson 2006). However, very few studies have assessed whether honeybees affect the development of bumblebee colonies, which might be more directly linked to reproductive success and fitness than the abundance of foraging bumblebees. Meeus et al. (2021) found that *B. terrestris* colonies gained more biomass at sites with a lower honeybee hive density than at sites with higher densities but did not show effects on reproductive success. Two other studies found reduced reproductive success of bumblebees in the vicinity of honeybee hives, one conducted within and the other outside of the native range of honeybees (Thomson 2004, Elbgami et al. 2014). However, it remains understudied how honeybee abundances relate to bumblebee fitness and whether competition between honeybees and bumblebees contributes to the decline of bumblebees. To fill this research gap, we conducted an experimental in-depth study in two regions in Germany on the competition between honeybees and bumblebees.

Hypotheses

With data collected on 304 Natura 2000 and other protected sites from the European field site network, we tested the hypotheses that species richness and densities of solitary bees and bumblebees are negatively related to honeybee densities, and that the negative relationship is steeper if flower availability is low at the local scale (low flower cover, flowering plant species richness, habitat area) and at the landscape scale (low habitat amount and high cropland cover).

In an in-depth study with 80 experimental bumblebee colonies in protected grasslands in Germany, we tested the hypothesis that the weight gain and the gyn production in *Bombus sylvarum* and *Bombus pascuorum* colonies decline with increasing honeybee densities in the surrounding grassland.

2. Methods

2.1. Study sites and geospatial analyses

Across 14 agriculturally dominated regions in 11 European countries, spanning from southern Spain to central Romania and from Southeast England to western Estonia (Figure 1), we selected 304 landscapes around a focal semi-natural pollinator habitat. These focal habitats differed across regions due to their location in different climatic and biogeographic zones, ranging from loess (Hungary) and calcareous grasslands (e.g. Germany, France, UK) to steppe fragments (Serbia) and forest grasslands (Spain). Based on the experience of local experts, the selected focal habitat types resembled the main pollinator refuge habitat in these landscapes, with habitats mostly protected under Natura 2000. Within each region, 20 to 30 landscapes (one exception with nine landscapes; average ± SE across all regions: 21.7 ± 1.5) were selected along gradients of habitat availability (same pollinator habitat as the focal habitat patch; henceforth ‘habitat amount’) and cropland cover, ranging from < 0.1 % to 93.9 % and 0 % to 89.6 %, respectively, in a radius of 2000 m surrounding the focal habitat patch across all regions. As cropland, we defined all land under recurring soil management. The area of the focal habitats differed across regions, ranging overall between 0.3 and 75.4 ha (14.6 ± 1.0 ha; average ± SE; for calculation, see below). For the in-depth study on bumblebee fitness, we selected ten calcareous grasslands sites in Lower Franconia and ten sites in Upper Franconia belonging to the field site network.

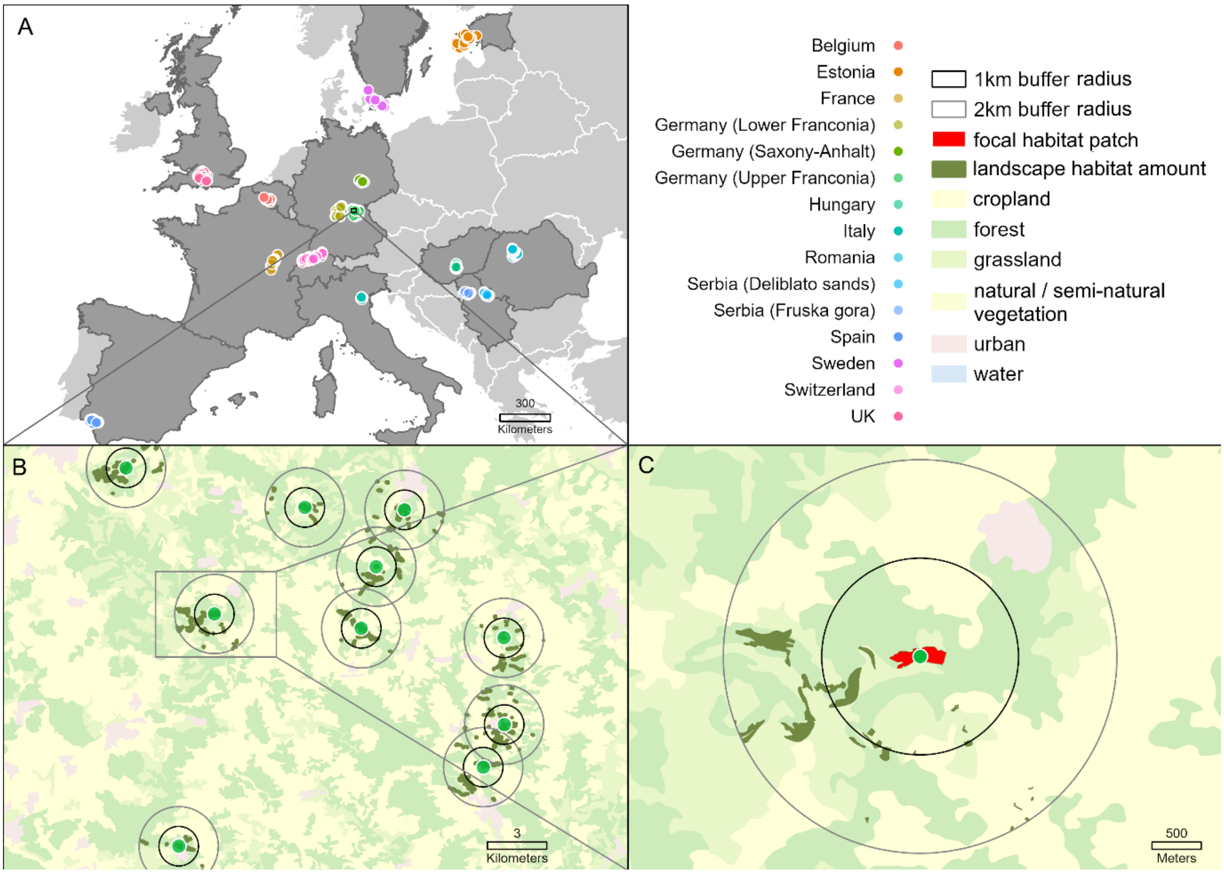

Figure 1: Map of the study regions of the Safeguard field site network, spanning the major European agricultural landscapes (A) with countries participating in the field site network highlighted in dark grey. With exception of Belgium all highlighted countries contributed data for assessing the relationship between honeybee and wild bee densities. Panels below show a subset of one of the study regions in Germany (Upper Franconia; B) with a detailed view of one of the landscapes (C) with the focal habitat patch indicated in red, habitat amount in the landscapes indicated in dark green, 1000m and 2000m buffer radii and coarse land-use classes indicated in pastel colours.

2.2. Pollinators and flower availability (European field site network)

In each focal habitat patch, we recorded pollinator densities and richness across three important bee pollinator groups differing in their ecology and behaviour, honeybees (*Apis mellifera*), bumblebees and solitary bees (Hymenoptera, Apiformes). The group of “solitary bees” included all non-*Bombus* wild bees, also (primitively) eusocial species of the genera *Lasioglossum* and *Halictus*). It can be assumed that the vast majority of honeybees came from colonies managed by beekeepers (Requier et al 2020), while all other bees were non-managed (“wild bees”). Pollinators were sampled in at least three sampling intervals, in some regions in up to six intervals (average ± SE: 3.6 ± 0.2) between 01 March and 29 September 2022. The number and timing of the sampling intervals were decided by local experts based on the geographical location and climate of the region, with regions further to the south sampled earlier then regions located to the north to account for macroclimatic phenology differences. Consulting local experts, the teams independently selected the timing and the number of sampling intervals that was expected necessary for a representative sampling of the local pollinator assemblages. Estimations of the sample completeness across taxa using the R package 'iNEXT.3D' (version 1.0.5, Chao et al. (2021)) confirmed an overall high sample completeness that was comparable across regions in both taxa (82.5 ± 1.7 percent in bumblebees, 71.3 ± 1.2 percent in solitary bees; average ± SE).

Within each interval, the order of sites sampled within each region was randomised and, on each site, we performed transect walks without fixed direction (30 min transect walk; speed: 16.7 m / min; 500 m transect length; sampling 1 m to each side of the transect; total area covered: 1000 m^2). Transects varied between intervals and transect walks covered different microhabitats as well as areas presumed beneficial to pollinators, e.g. patches of wildflowers or bare ground. Transect walks were performed between 9 am and 5 pm with good weather conditions (> 13°C in the sun, wind < 3 bft, no rain) and each site was sampled at least once in the morning, noon and afternoon across the different sampling intervals. Each transect was walked by the same observer and specimens were caught using a sweep net, identified in the field wherever possible and subsequently released. If no identification was possible in the field, specimens were collected for identification in the lab. For all analyses, pollinator species richness was accumulated across sampling intervals while pollinator density was calculated as pollinator individuals observed per sampling interval.

As measures of pollinator-related habitat quality, we recorded the flower cover and the number of flowering plant species richness along the bee transects during each pollinator sampling interval. Data for plant species richness was not available for the regions in Hungary, Italy and Spain. These regions were hence excluded from all analyses that flower cover and plant species richness included (retaining 234 landscapes in these models). In the analysis, we used accumulated plant species richness across the sampling intervals.

2.3. Bumblebee fitness in experimental colonies (in-depth study)

We placed four wooden nesting boxes for bumblebees on each of the 20 sites in two regions in Germany (Lower and Upper Franconia; total of 80 boxes). In April, *Bombus pascuorum* and *Bombus sylvarum* queens were caught in the regions and placed in rearing boxes in a climate chamber. After visual screening for ectoparasites, they were constantly supplied with sugar water and fresh pollen and paired to stimulate breeding (following Ptáček et al. 2015). When colony size reached a minimum of three workers and additional brood cells were close to hatching, they were transferred to the field and placed in the wooden nesting boxes. Transfer of the colonies took place from early May to early June. Two *B. sylvarum* and two *B. pascuorum* colonies were placed in each study site.

After successful establishment of the colonies in the field, they were monitored throughout the season. We assessed the maximum weight gain of each colony ('peak weight') as a measure of colony development. In addition, we measured the reproductive success by counting the queens and males in the colony, took photos of the nest and screened the nests for parasite infestation. These measurements were done monthly until end of September when the season came to an end, meaning colonies lost weight and only had queen and male brood left. Based on this data, we calculated a reproductive success index, accounting for the different 'value' of queens compared to males. The calorific value ratio of males to queens is roughly 1:3.3 (Beekman und van Stratum 1998). So, here the number of queens were counted 3-fold and were combined with the onefold number of males to calculate a reproductive success index.

To record honeybee abundances, transect walks were performed on the grasslands where the bumblebee colonies were placed.

Honeybee transects were conducted monthly at the same days as the bumblebee colonies were monitored. In a 30-minute walk, all honeybees were recorded on a transects with 750 m length, and 2 m width. Transect surveys were only conducted during suitable weather conditions. Honeybee densities were summed across the season.

2.4 Statistical analyses

All statistical analyses were performed in R 4.4.1 for Windows (R Development Core Team 2024). In a first step, we assessed the relationship between honeybee densities and wild bees across all 304 landscapes with Pearson correlations. All bee variables were log-transformed after adding 0.1 to avoid zero-values.

In a second step, we tested whether the flower variables recorded at the local scale affected the relationship between honeybees and wild bees. We fitted generalised mixed effects models (GLMMs; package ‘glmmTMB’, version 1.1.10 (Brooks et al. 2017)) with the response variables species richness and density of solitary bees and bumblebees, the fixed effects (1) honeybee density (continuous), (2) species richness of flowering plants (continuous), (3) local flower cover (continuous), (4) the interaction between honeybee density and species richness of flowering plants and (5) the interaction between honeybee density and flower cover. In a third step, we tested whether further variables which might be related to flower availability affected the relationship between honeybees and wild bees. We fitted generalised mixed effects models with the response variables species richness and density of solitary bees and bumblebees, the fixed effects honeybee density and either (1) focal patch area (continuous), (2) habitat amount in the landscape (continuous), or (3) cropland cover in the landscape (continuous), as well as the two-way interaction. To account for varying species richness and densities between study regions, these models contained a random intercept on ‘study region’. All models mentioned above were fitted using a Gamma hurdle model with log-link.

In all models, all continuous predictors were centred at their average and scaled to multiples of their standard deviation (z-scaling) prior to model fitting. Model fits were inspected visually and using various diagnostic tests with the package DHARMa (version 0.4.7 (Hartig 2022)). Model outputs were obtained using type III sums of squares Wald chi-square tests with the command ‘Anova’ (library ‘car’, version 3.0-12 (Fox and Weisberg 2019)).

The relationships of honeybee densities with bumblebee fitness (measured as peak colony weight and reproductive success index) were assessed with Pearson correlations.

3. Results

Across all regions, we recorded 9775 honeybees, 13239 solitary bees (500 species) and 7502 bumblebees (29 species). On average 7.4 ± 0.7 honeybees, 11.0 ± 0.6 solitary bees and 8.1 ± 0.5 bumblebees were recorded in each sampling interval. Honeybee density recorded per site and sampling interval varied considerably within and across regions resulting in overlapping density gradients across regions. (Figure 2).

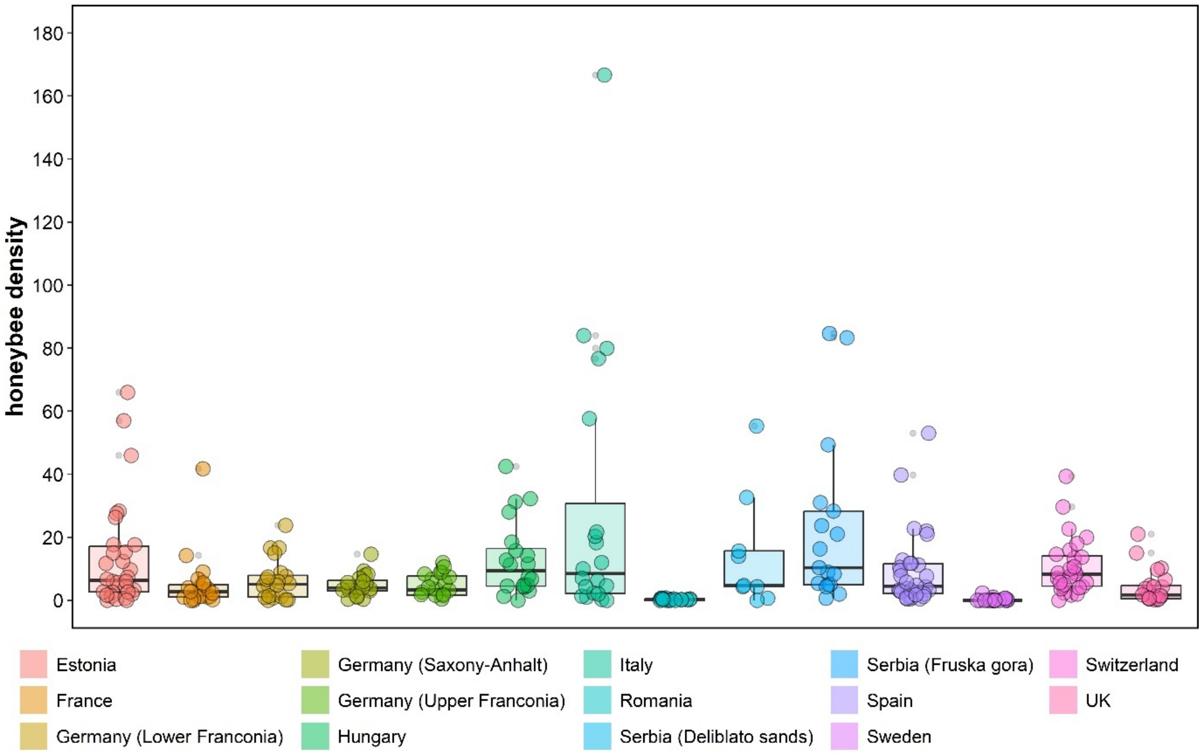

Figure 2: Honeybee densities per site and sampling interval across regions.

In models with honeybee densities as only fixed factor, we found an overall positive relationship between honeybee density and solitary bee density, but slopes differed among regions (Figure 3). Overall bumblebee density and species richness of both solitary bees and bumblebees were not related to honeybee density in these models, but negative slopes occurred for bumble bee densities in some countries (Figure 3).

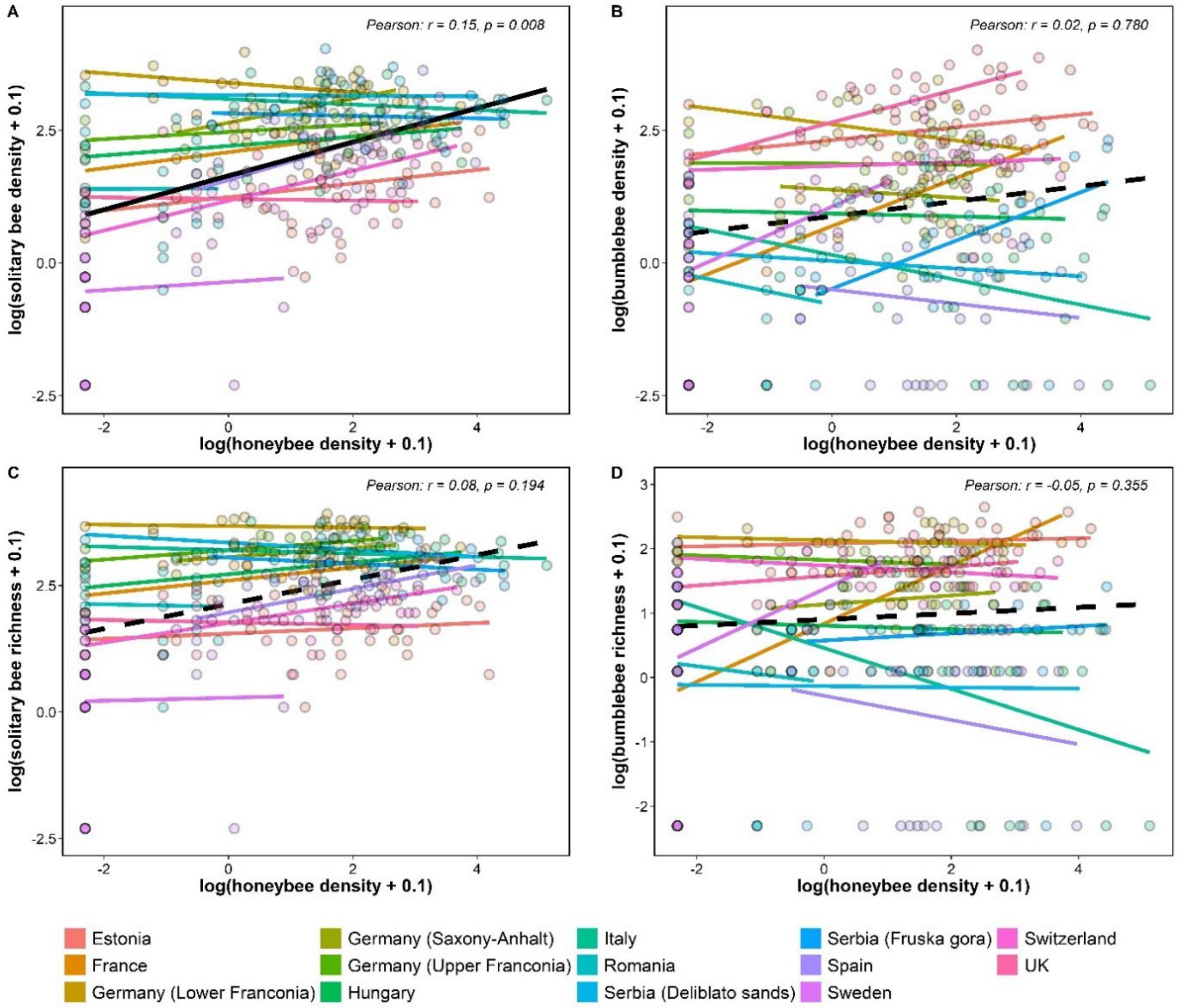

Figure 3: Relationships between honeybee density and (A) solitary bee density, (B) solitary bee species richness, (C) bumblebee density and (D) bumblebee species richness. Black lines show overall effects (solid black line: $p < 0.05$, dashed black line: $p > 0.05$). Coloured lines show correlations for each separate study region, irrespective of whether these were statistically significant or not.

In models assessing the interaction of honeybee densities with local flower variables, we found no significant interaction with flowering plant species richness and flower cover. Species richness and density of solitary bees increased with flowering plant species richness, bumblebee species richness with both plant species richness and flower cover, and bumblebee density with flower cover. Additionally, densities of both bumblebees and solitary bees were positively related to honeybee density (Table 1).

In models assessing the interaction of honeybee densities with further environmental variables that are potentially related to flower availability, neither the interactions nor the fixed effects of local patch area, landscape-scale habitat amount and cropland cover in the landscape were significant (all $p > 0.05$).

Table 1: Results from GLMMs with the response variables species richness and density of solitary bees and bumblebees and the fixed effects honeybee density, species richness of flowering plants, local flower cover and the interactions between honeybee densities and flower variables. Arrows indicate significant positive relationships ($p < 0.05$). *** $p < 0.001$, * $p < 0.05$, (*) $p < 0.1$.

	solitary bee		bumblebee	
	richness	density	richness	density
Honeybee density		* ↗		* ↗
Plant species richness	*** ↗	*** ↗	* ↗	(*) ↗
Flower cover	(*) ↗		* ↗	*** ↗
Honeybee density : Plant species richness		(*)		(*)
Honeybee density : Flower cover				

Although honeybee abundances strongly differed among the grassland sites where the bumblebee colonies were located, neither peak weight of the bumblebee colonies nor the reproductive success index were related to the honeybee abundances (Figure 4). Thus, we did not find any indication of competition between honeybees and bumblebees in protected grasslands.

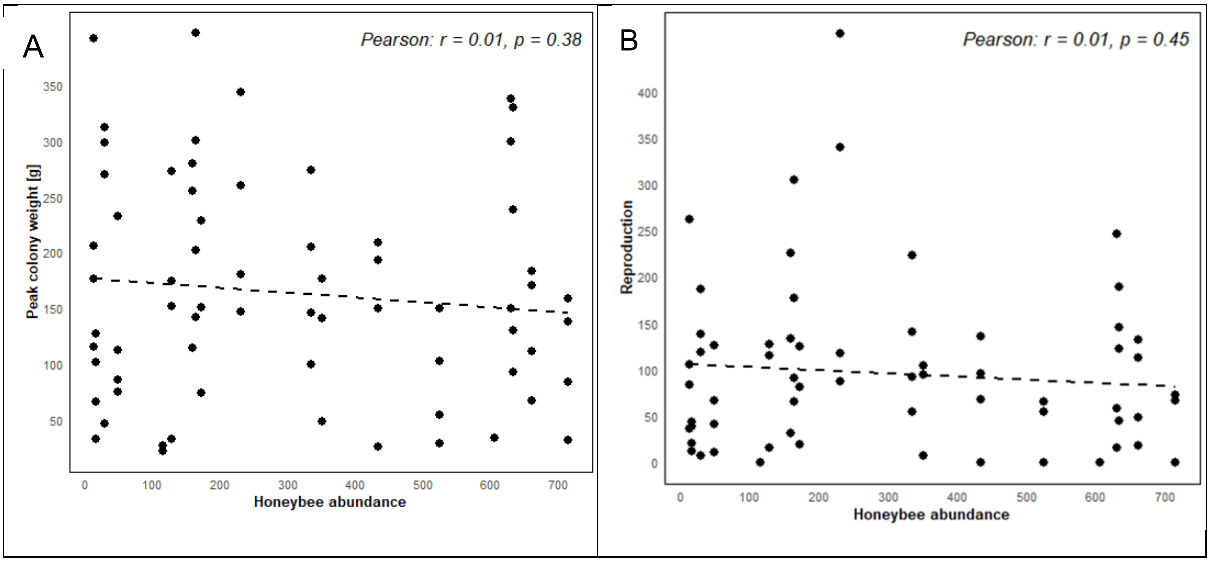

Figure 4: Relationship between honeybee densities and (A) peak colony weight and (B) reproductive success index in experimental bumblebee colonies of *Bombus sylvarum* and *B. pascuorum* on calcareous grasslands. The reproductive success index accounts for differences in the calorific value of bumblebee queens and males by counting the number of queens 3-fold and the number of males onefold.

4. Discussion

Across the 304 sites of the European field site network, we did not find any evidence for competition between honeybees and solitary bees or bumblebees. Neither species richness nor densities of solitary bees and bumblebees were negatively related to honeybee densities across the 14 study regions. Thus, our results do not confirm the negative relationship between honeybee and bumblebee densities found in heathlands in the UK (Forup & Memmott 2005).

Preconditions of competition between honeybees and wild bees is that pollen or nectar resources are limited, and that bees overlap in their resource use (Sponsler et al. 2023). A negative relationship between densities of honeybees and wild bees in the foraging habitat can be an indication for exploitative or interference competition. While exploitative competition can arise if plants cannot provide enough pollen or nectar for all visiting bees, interference competition can arise if (1) a bee does not visit a flower that is currently visited by another bee or (2) a bee interrupts foraging and leaves a flower earlier because another bee lands on the flower (Greenleaf & Kremen 2006). In contrast, interference competition though aggressive behaviour seems to be very rare and should not have significant consequences in honeybee-wild bee interactions (Cairns et al. 2005, Frankie et al. 2005).

Both exploitive and interference competition will result in a negative relationship between the densities of the competitors if competition is asymmetric. Competition will force the inferior competitor to invest more time in the search for alternative food resources and might thus reduce the total intake of nectar or collection of pollen, and consequently fitness (Butz Huryn 1997, Sponsler et al. 2023). There are several reasons to assume that the competition between honeybees and wild bees is asymmetric and that wild bees are the inferior competitors. Due to their large colonies with 20,000 to 60,000 workers, honeybee densities can easily surpass wild bee densities in the foraging habitat, they harvest large quantities of floral resources from various plant species, and they are active throughout the warm season (Geslin et al. 2017). Furthermore, honeybees are more efficient in the exploitation of available resources due to intra-colony communication (Nürnberger et al. 2017. This allows a strong honeybee colony to gather as much pollen as the solitary bee *Megachile rotundata* requires to produce 100,000 progenies (Cane and Tepedino 2016). Thus, it is expected that high densities of honeybees result in competition with wild bees and a decline in wild bee densities and species richness.

The absence of a negative relationship between honeybees and wild bees across the European field site network can have several reasons. One explanation is that flower resources were not limited across the study sites. However, our data on nectar depletion rates indicate that at least during a dry summer nectar was strongly limited on calcareous grasslands (Sponsler et al. 2024a). A second explanation is that there was no overlap in resource use of honeybees and wild bees. While the niche overlap of honeybees with generalist bumblebee species is generally very high (Thomson 2006; Franco et al. 2009), the overlap with solitary bees can be lower, especially for small and more specialized species (Weaver et al. 2022). A third explanation is that the limitation of flower resources and the resource overlap of honeybees and wild bees differed among sites, and thus competition only occurs in a subset of some sites.

To go a step further in our understanding of honeybee-wild bee competition, we assessed how environmental variables that potentially affect flower limitation and niche overlap modulate the relationship between honeybee densities and wild bees. We therefore tested whether there are interacting effects of honeybee densities and environmental variables on wild bees.

4.1. Interacting effects of honeybees and environmental variables

Across the European field site network, we found no interactions between honeybee densities and environmental variables on density and richness of solitary bees and bumblebee. The lack of significant interactions suggests that the relationships between honeybees and wild bees were not modulated by the environmental variables, and that competition was absent across the covered gradients of each of the environmental variables in our study. This was contrary to our expectation that negative relationships between honeybees and wild bees are steeper on sites with low flower cover, species richness and patch area at the local scale, and with lower landscape-scale habitat amount and larger cropland cover at the landscape scale. In detail, we expected that the probability of negative honeybee-wild bee relationships in enhanced on sites with low flower availability at the local scale because the risk of resource limitation increases (1) with decreasing flower cover leading to a reduced amount of nectar and pollen, and (2) with decreasing species richness of flowering plants, because species-rich plant communities enhance the pollinators` chance of finding their preferred plants, i.e. the plant species whose nectar and pollen the pollinator species can use best. Furthermore, high species richness of flowering plants might reduce niche overlap in species-rich plant communities, because bees can more easily switch to other plant species of similar value in the presence of other flower visitors and thus reduce the overlap of the realized niche (“interactive complementarity”; Fründ et al. 2013). Additionally, resource limitation might decrease with increasing area of a habitat patch, because larger patches provide higher habitat heterogeneity with a larger species richness of flowering plants and a larger total amount of flowers than small habitat patches.

As bees usually forage at larger than local scales, we also focused on environmental variables that are related to flower availability at the landscape scale. However, neither the landscape-scale habitat amount (i.e. the amount of the habitat type of the focal patch), which should be positively related to landscape-scale flower availability, nor cropland cover, which should be negatively correlated, modulated the relationships between honeybee densities and wild bees. Thus, we conclude that across the studied gradients, the risk of competition between honeybees and wild bees did not increase with decreasing local and landscape-scale flower availability.

4.2. Positive relationships between honeybees and wild bee densities

Interestingly, we found a positive relationship between honeybee density and densities of solitary bees and bumblebees, even though flowering plant richness and flower cover were included in the models to control for shared responses of honeybees and wild bees to these flower variables.

Our results thus suggest that there was a strong overlap in the food resources used by honeybees and wild bees. This overlap did not only exist because both honeybee and wild bee densities positively responded to an increase in flowering plant species richness and flower cover, because otherwise the positive relationship should have disappeared in the presence of the control variables. Thus, additionally other shared responses to variables that were not tested resulted in a positive relationship between the pollinator groups e.g., shared preferences for certain plant species within the plant community or shared responses to nectar or pollen amount or quality. We conclude from our results that honeybees and wild bees foraged in the same plant communities without reducing the densities of the other pollinator group. Species richness and densities of solitary bees and bumblebees increased with increasing species richness of flowering plants and flower cover. Thus, we conclude that enhancing local flower availability is more important to promote wild bees than reducing honeybee densities.

4.3. Effects of honeybees on bumblebee fitness

With an experimental study in Germany, we show that weight gain and gyn production in bumblebee colonies did not decline with increasing honeybee densities in the surrounding grassland. Thus, we found no indication of competition between honeybees and *Bombus pascuorum* and *Bombus sylvarum* in protected grasslands. Niche overlap between honeybees and generalist bumblebee species is generally high (Thomson 2006; Franco et al. 2009) Furthermore, bumblebees are limited by floral resource availability, as shown in a previous study where supplemental feeding improved colony performance (Requier et al. 2020). Thus, the risk of honeybee-bumblebee competition is high, and more probable than between honeybees and solitary bees, whose resource overlap is much smaller for most species (Weaver et al. 2022). Several previous studies suggested that honeybees and bumblebees interact while they forage. Bumblebee worker densities decreased with decreasing distance to honeybee colonies (Thomson 2006), bumblebee's preference for the most abundant floral resource was reduced by increasing honeybee densities (Thomson 2021), and bumblebee workers were significantly smaller in areas where honeybees occurred (Goulson & Sparrow 2009) showed that Longer tongued bumblebee species switched to different plant species close to honeybee hives while short-tongued bumblebees such as *Bombus terrestris* avoided foraging in areas close to honeybee hives (Walther-Hellwig et al. 2006). However, these results do not show whether these interactions led to reduced reproductive success and thus fitness disadvantages for bumblebees. An indirect indication for reduced reproductive success comes from Thomson (2021) who showed that honeybee abundance negatively correlates with bumblebee abundance in the following year. Similarly, adding honeybee hives to flower strips counteracted the positive effects of these strips on the abundance of foraging bumblebee queens in the following year (Bommarco et al. 2021).

Very few studies have assessed whether honeybees affect the development of bumblebee colonies, which might be more directly linked to reproductive success and fitness than the abundance of foraging bumblebees. One of these studies found that *B. terrestris* colonies gained more biomass at sites with a lower honeybee hive density than at sites with hive higher density but did not show effects on reproductive success (Meeus et al. 2021). In two other studies, reproductive success of bumblebees was reduced in the vicinity of honeybee hives. One of these studies was conducted within, the other outside of the native range of honeybees (Thomson 2004, Elbgami et al. 2014). We conclude from our study that competition between honeybees and bumblebees might not be as common as suggested in the previous literature, particularly studies not reporting fitness data might overestimate the impact of honeybees on bumblebees. Our data strongly suggest that a decline of bumblebees is rather related to a decline of flower cover and flower species richness than to an increase in honeybee densities.

4.4. Implications for the conservation of wild bees

We did not find any signs that indicate competition between wild bees and honeybees despite a more than hundred-fold variation in the density of foraging honeybees in our study sites. Solitary bee and bumblebee densities were positively related to honeybee densities, even after controlling for shared responses to flower cover and species richness of flowering plants. Thus, our data suggest a strong overlap in resource use between honeybees and wild bees but do not provide evidence for competition. We conclude from our study that reducing honeybee densities in and around valuable wild bee habitats (e.g. by reducing the number of honeybee colonies or by banning honeybee colonies from a buffer around valuable bee habitats) is a justified measure from a precaution perspective, but with low chance to enhance wild bee density and richness in these habitats. Instead, we urgently need conservation measures that improve local habitat quality by enhancing flowering plant species richness and nesting sites (Biegerl et al. 2025, Boetzl et al. 2025). Besides, improving the quality of agricultural landscapes should have the highest priority: Agricultural landscapes with small field sizes and a high proportion of organic farming benefit wild bees in Natura 2000 and other highly protected bee habitats that are imbedded in these landscapes (Biegerl et al. 2025) and should also support honeybees with additional resources while reducing shortage of pollen and nectar for potential inferior wild bee species.

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6. References

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