# Competition between managed honeybees and wild bumblebees

## Quantifying dietary overlap in semi-natural grasslands

**EMMA ROSBERG 2023**
**MVEK12 EXAMENSARBETE FÖR KANDIDATEXAMEN 15 HP**
**MILJÖVETENSKAP | LUNDS UNIVERSITET**

# Competition between managed honeybees and wild bumblebees

## Quantifying dietary overlap in semi-natural grasslands

Emma Rosberg

2023

# Abstract

The decline of bees, such as bumblebees, over the last decades raises concerns as they are key pollinators in both agricultural and natural ecosystems. One proposed cause for the decline of wild bees is competition for food resources with managed honeybees. Detrimental effects of competition can result where co-existing species exhibit a high degree of shared resource use (i.e., niche overlap). The aim of this study was to assess the degree of niche overlap between honeybees and six bumblebee species in semi-natural grasslands, which are important bee conservation habitats. This study examined the degree of niche breadth (i.e., species richness of foraged plants visited by each bee species) and explored if plant functional richness (flower colour and shape) and bumblebee tongue length structured niche overlap. This was undertaken by analysing data collected from 32 pastures, in 8 different landscapes in Skåne between May and July 2022. Data consisted of all flower visiting honeybees and bumblebees and the visited plant species observed during transect surveys. Differences in niche breadth between honeybees and bumblebees were analysed using generalised linear models. Differences in niche overlap with honeybees between bumblebee species, as well as in relation to plant functional richness and bumblebee tongue length were analysed using linear models. Honeybees and *B. terrestris* foraged on more plant species than the other bumblebee species. Niche overlap with honeybees varied between bumblebee species. Niche overlap decreased with increasing tongue length and with increasing plant functional richness. Therefore, competition with honeybees is most likely to occur among short-tongued bumblebee species which exhibit the highest niche overlap. Increasing or maintaining plant functional richness in semi-natural grasslands has the potential to reduce competition between honeybees and bumblebees, by decreasing niche overlap and underscores the importance of ongoing conservation of semi-natural grasslands, to help mitigate against ongoing wild bee declines.

# Populärvetenskaplig sammanfattning

Under de senaste årtiondena har bin, såsom humlor, minskat i både antal arter och populationsmängder. Detta är ett stort problem för vårt samhälle då både jordbruket och naturliga ekosystem till stor del är beroende av dessa pollinatörer. Det är speciellt problematiskt att humlor minskar då de har förmågan att utföra en speciell sorts pollinering (buzz-pollination) som några av våra vanligaste grödor så som potatis och tomater kräver för framgångsrik pollenöverföring. Flera orsaker har presenterats som förklaringar till humlornas nedgång, alltifrån förluster av habitat till sjukdomar. Men även konkurrens från honungsbin har presenterats som en möjlig orsak, till exempel konkurrens om föda. Konkurrens om föda kan studeras genom att undersöka om det finns ett överlapp mellan humlornas och honungsbinas så kallade nischer. Om det finns ett överlapp i nischer betyder det att den undersökta humlearten och honungsbin delvis samlar in föda på samma växtarter och därmed finns det en konkurrens om föda mellan dem.

Syftet med den här studien var att bedöma graden av nischöverlapp mellan honungsbin och sex humlearter i halvnaturliga gräsmarker, vilka är viktiga livsmiljöer för bevarande av bin. Därtill undersökte studien arternas nischbredd, det vill säga antalet växtarter som besöktes av varje art av bi. Slutligen undersöktes om växtfunktionell rikedom (baserat på blommors färg och form) och humlors tunglängd strukturerar potentiellt nischöverlapp. Växtfunktionell rikedom kan ses som ett mått på mängden mångfald ett område innehöll, här sett till blommornas färg och form.

Undersökningen gick ut på att analysera data som samlats in från 32 betesmarker, i 8 olika landskap i Skåne mellan maj och juli 2022. Data bestod av alla blombesökande honungsbin och humlor och de besökta växtarter som observerats vid transektundersökningar. Skillnader i nischbredd mellan honungsbin och humlor analyserades med hjälp av generaliserade linjära modeller. Skillnader i nischöverlapp med honungsbin mellan humlor, samt i förhållande till växtfunktionell rikedom och humlors tunglängd analyserades med hjälp av linjära modeller.

Resultatet var att honungsbin och *B. terrestris* sökte föda på fler växtarter än de andra humlearterna, därmed hade de bredast nisch. Vidare var resultatet att nischöverlappet med honungsbin varierade mellan humlearterna. Studien fann att överlappet i nisch minskade ju längre tunga en viss humleart hade i förhållande till honungsbin. Därtill fann studien att för alla humlearter minskade överlappet i nisch ju mer mångfald ett område innehöll sett till blommornas färg och form, det vill säga vid större växtfunktionell rikedom. Studien indikerar att det är mest sannolikt att

konkurrens med honungsbin förekommer bland korttungade humlor, som har störst nischöverlapp med honungsbin. Därtill dras slutsatsen att öka eller bibehålla växtfunktionell rikedom i halvnaturliga gräsmarker har potential att minska konkurrensen mellan honungsbin och humlor, genom att minska nischöverlappet. Därmed understryks vikten av att bevara områden med hög biologisk mångfald, såsom halvnaturliga gräsmarker, för att motverka att humlor utkonkurreras av honungsbin och på så sätt bidra till att minska nedgången av vilda bin.

# Table of contents

# 1. Introduction

Pollination by bees, including bumblebees, provides a crucial ecosystem service to our societies and our ability to feed an ever-growing population. 85% of all flowering plants (Ollerton et al., 2011), and up to 2/3rds of crops benefit from pollination for successful reproduction and fruit development (Klein et al., 2007). Thereby the decline of bee populations over the last decades (Goulson et al., 2015) raises concerns and calls for explanations. Several causes including habitat loss, disease, and pesticides (Goulson et al., 2015) have been raised. However, competition between invasive and/ or managed bees and wild bees has also been suggested as an explanation for losses of native bees (Goulson, 2003). Losses of native bees cause losses of biodiversity and abilities to pollinate different kinds of plants, as pollination abilities are dependent on the morphology of the bee as well as plant traits (Cappellari et al., 2022). Given that wild native bees are often more effective pollinators than managed honeybees (Page et al., 2023), understanding the causes of native bee biodiversity loss is crucial to maintaining ecosystem functioning and services related to pollination.

Competition between different bee species can be one cause of native bee biodiversity loss. Competition between bees is affected by their niche, i.e., an animal's place in its environment, often in relation to food and enemies (Whittaker et al., 1973). Species can exhibit niche overlap where they share resources. However, according to the exclusion principle two species cannot occupy the same niche in the same geographical area, if so one species will always outcompete the other (Hardin, 1960). Thereby, competition will result in niche differentiation, i.e., species will alter their niche to allow co-existence (Hardin, 1960). Since overlap in niches may result in competition, it is important to investigate niche overlap to understand competition between managed bees and wild bees.

Several studies have examined the effects managed honeybees can have on wild and native bees (Cane & Tepedino, 2017; Goulson, 2003; Rasmussen et al., 2021; Ropars et al., 2022; Steffan-Dewenter & Tscharntke, 2000). One such effect is competition for food resources (Goulson, 2003). Honeybees are considered generalists (Cappellari et al., 2022) making other generalist bee species more prone to food resource competition. This applies for bumblebees, as most species are considered generalists, which enables bigger chances of niche overlap with honeybees (Wood et al., 2021). Secondly, honeybee colonies are substantially larger in numbers compared to bumblebee species and therefore require more resources. Cane and Tepedino (2016) found that during three summer months a typical apiary of honeybees

collects pollen equivalent to four million wild bees. In short, there are several reasons that increase the risk of competition for food resources between honeybees and bumblebees. In line with this, Ropars et al. (2022) found competition between bumblebees and honeybees when examining the temporal dynamics of food resource competition between honeybees and wild bees, including bumblebees. They concluded that food resource competition is strongest during early spring and then declines during the season. When examining interspecific competition between honeybees and wild bees in Germany, Steffan-Dewenter and Tscharntke (2000), found that resource overlap between honeybees and wild bees was 45.5%. However, they did not find significant correlation between abundance of species richness of wild bees in relation to honeybee colonies or density of flower-visiting honeybees. Similarly, Rasmussen et al. (2021) found no significant relationship between overlap with honeybees and forage specialisation when comparing pairwise niche overlap for individual bee species. But they found that 200 out of 292 wild bee species in Denmark had more than a 70% overlap of their forage plants with honeybees. When Elliot et al. (2021) examined niche overlap in protected areas in Australia, they found general niche overlap between honeybees and native bees (0.43), with the strongest overlap with native stingless bees (0.70). In summary it has been proven that niche overlap between honeybees and wild and/or native bees, such as bumblebees, occurs worldwide but consequences of niche overlap on e.g., population and foraging behaviour have been more difficult to prove. Given the large resource requirements of honeybee colonies, in conjunction with the shared resource use with wild bees, competition between wild bees and honeybees has the potential to detrimentally affect wild bee populations and/or communities.

Niche overlap can be dependent on plant and pollinator traits, since, as stated earlier, both morphology of the bee and the plant affect pollination possibilities. (Cappellari et al., 2022). Cappellari et al. (2022) found that only in plant communities with high functional diversity, i.e., high availability of plant traits, resource overlap between wild pollinators and honeybees decreased with increasing honeybee abundance. Thereto, resource overlap increased with increasing trait similarity between wild pollinators and honeybees, the more similar proboscis length a pollinator had in comparison with honeybees the more overlap. Thereby, Cappellari et al. (2022) depicts that pollinator and plant traits can affect the structure of niche overlap which emphasizes the importance of investigating such affects when studying food resource competitions between honeybees and bumblebees.

Habitats can also affect bumblebee species chances of survival and in bee conservation semi-natural habitats has been stated to be of great importance (Öckinger et al., 2007; Raderschall et al., 2021). Semi-natural habitats, such as grasslands, are of importance since they provide nesting and floral resources, often in agriculture environments where stressors such as pesticides are present (Öckinger et al., 2007). The presence of semi-natural grasslands has been found to increase abundance and species richness of bumblebees in nearby habitats (Öckinger et al., 2007). Given semi-

natural habitats positive effects on bumblebee diversity, examining niche overlap in semi-natural grasslands is of significance to give further insight into the decline of bumblebees.

This study focuses on dietary niche overlap, i.e., competition between honeybees and different species of bumblebees for food resources. It examines how plant and pollinator traits can affect the structure of niche overlap, in this case between honeybees and bumblebees. It will provide an example from Sweden and from semi-natural grasslands, adding novel information alongside previous studies that have looked at cropland (Lindström et al., 2018) to increase our understanding of the mechanisms behind bumblebee decline.

## 1.1 Purpose and research questions

### 1.1.1 Purpose

The purpose of this study is to examine if there is food resource competition between bumblebees and honeybees, by studying the degree of niche overlap between bumblebees and honeybees. Furthermore, the study aims to investigate differences in niche breadth between bumblebees and honeybees, by examining interspecific differences in the number (richness) of different plants foraged on. The study will also explore if plant and pollinator traits could be an explanation to structure of potential niche overlap.

### 1.1.2 Research questions

- How much species richness does the different bees have in their plant foraging?
- How much niche overlap is there between honeybees and bumblebees in semi-natural grasslands?
- Is the degree of niche overlap between honeybees and bumblebees affected by pollinator and/or plant traits?

## 1.2 Delimitations

The study has been delimited to focus on comparing niche overlap between bumblebee species and the honeybee species *Apis mellifera* and not comparing niche overlap between bumblebee species.

Examining plant and pollinator traits as potential explanations to structure of niche overlap have been delimited to focus on two floral traits: flower type (e.g., open, tube) and flower colour, and one pollinator trait: tongue length.

The study's data set was gathered during several months (late May – end of July) but analysis will focus on overall effects, and not explore temporality. In addition, analyses will not be performed on all species that were found in the field but will be delimited to six bumblebee species that were frequent enough in the collection that statistical analyses were considered appropriate.

## 1.3 Environmental relevance

As mentioned, bees, such as bumblebees, are of great importance to human society as they provide the essential ecosystem service of pollination, which is needed to feed the world's population. Bumblebees are of extra importance through their ability to perform buzz pollination (Cooley et al., 2021), a special kind of pollination that some of our most frequent crops such as potatoes and tomatoes require for successful pollen transfer (De Luca & Vallejo-Marín, 2013). Worth mentation is that *A. mellifera* cannot perform buzz pollination. Thus, mechanisms behind bumblebee losses are of great importance to investigate from an environmental perspective.

## 1.4 Ethical reflection

The bumblebees, except for *Bombus terrestris*, gathered during data collection were collected and killed to facilitate their identification in the lab. Another consideration is if the bumblebee species are a part of the Swedish "Rödlistan" (SLU Artdatabanken, 2020), which classify species that are endangered to different degrees. This is the case for *Bombus muscorum*. However, as the data used in this study already had been collected, these ethical dilemmas did not affect the method of the study.

The results of the study could potentially be used to argue that honeybees can be harmful, and should not be managed, thereby possibly affecting beekeepers' livelihoods. Therefore, conclusions have been carefully drawn. On the other hand, research to further understand how our actions by managing honeybees could harm an already impacted ecosystem service is important. Especially considering pollinators' crucial role in agriculture.

# 2.  Method

The study was an analysis of data collected in previous field trials, carried out between May and July 2022 in Skåne (Kendall, Bernhardsson & Smith, 2022).

## 2.1 Data Collection - Field trials

The field trials were carried out between late May and end of July 2022 in eight different landscapes in Skåne (Kendall, Bernhardsson & Smith, 2022). In each landscape, four pastures were selected; in the first one, a large apiary with 10 beehives was placed, and the rest were at 500, 1000 respectively 2000 metres from the first pasture. This was done to enable exploration of honeybee density changes with distance from the beehive, however this study will not take density changes into account. The results could also be affected by the fact that in each pasture two bumblebee colonies of *B. terrestris* was placed. This was done to study effects on reproductive success, however that is not studied in this study.

To assess bee foraging patterns Kendall, Bernhardsson and Smith undertook transect surveys once every 10th day in each pasture, one landscape per weekday, from the end of May to the end of July. This resulted in a total of four rounds per pasture during the whole season. Transect survey duration ranged from 20 - 40 minutes per pasture with the length difference depending on floral densities within pastures. Lower floral densities resulted in longer transects. The surveyor walked along the transect at a slow walking pace and noted all flower visiting individuals of honeybees, *B. terrestris* and wild bees (including bumblebees) as well as the plant species they were found on within a metre on each side of the transect. The flowering plants, honeybees, and *B. terrestris* were identified in the field whereas the bumblebees were collected directly from the flowering plants using a sweep net, then frozen and identified later in the lab.

## 2.2 Analysis

All data analysis and figures compared between the honeybee species *A. mellifera* and the different bumblebee species were undertaken using "R" version 4.2.3 (R Core Team, 2023). The significance level for all tests was 0.05.

### 2.2.1 Diet breadth

Differences in diet breadth (i.e., the species richness of plants foraged on by different bee species) was compared by calculating the total diet breadth (across all sites) for each species, as well as the site-specific diet breadth for each species. Differences between species were then tested using a generalised linear model, specified with a Poisson distribution. Model residuals were tested and deemed acceptable using the tests for dispersion and normality within the R package "DHARMa" (Hartig, 2022). A post-hoc Tukey's Honest Significant Difference (HSD) test was performed to test if plant richness differed significantly among the different bee species.

### 2.2.2 Statistical analysis of niche overlap

Niche overlap between *A. mellifera* and the different species of bumblebees was quantified for each site by using the R package "EcoSimR" (Gotelli et al., 2015). EcoSimR uses a null model analysis to assess if the calculated niche overlap is more or less than would be expected by chance, i.e., what would be expected if species used, in this case, flowering plants independently of one another. A null model is a model that randomize ecological data or random samples from a hypothetical or known distribution to generate patterns that would be anticipated if a specific ecological mechanism were absent (Gotelli & Graves, 1996).

The niche overlap was calculated using the niche overlap function comparing each bumblebee species with *A. mellifera* at each site. The metric used was Pianka (Pianka, 1973) and the randomization algorithm used was RA3, as it is the recommended algorithm given its statistical properties (Gotelli, et al., 2015). The niche overlap was given by the standardised effect size (SES), i.e., the magnitude of observed niche overlap relative to average random values (n = 1000) of niche overlap. The SES was in turn calculated as a Z-transformed score according to following formula (Ulrich & Gotelli, 2007):

$$Z = \frac{(x - \mu)}{\sigma}$$

Where x denotes observed index, $\mu$ denotes mean, and $\sigma$ denotes standard deviation of the 100 index values from the simulated matrices (Ulrich & Gotelli, 2007).

SES below -2.0 or above 2.0 is considered statistically significant, i.e., a value above 2.0 means there is statistically significant niche overlap and a value below 2 means there is statistically significantly lower niche overlap then by chance (Ulrich & Gotelli, 2007).

### 2.2.2.1 Niche overlap in relation to bumblebee species

Differences in niche overlap between bumblebee species was tested using a linear model. Model residuals were tested and deemed acceptable using the tests of dispersion and normality within the R package "DHARMa" (Hartig, 2022). A post-hoc Tukey HSD test was performed to test if niche overlap differed significantly among the different bumblebee species.

### 2.2.2.2 Niche overlap in relation to tongue length

The effect of pollinator traits on niche overlap were explored by modelling niche overlap as a function of the difference in tongue length between *A. mellifera* and each bumblebee species. The difference in tongue length for each species of bumblebee was calculated according to the following formula:

$$Difference\ in\ tongue\ length = Bumblebee\ tongue\ length - Honeybee\ tongue\ length$$

Persson et al. (2015) was used as the source for all bumblebee species' tongue length except *B. muscorum*, as it was not included. Persson et al. (2015) was used as it contained tongue length data from Skåne, Sweden, and therefore, came from similar environmental conditions to this study. For *B. muscorum* Arbetman et al. (2017) was used as the source for tongue length, which in turn calculated the tongue length as a mean from Harmon-Threatt et al. (2013), Williams et al. (2009), and Goulson et al. (2005). Cariveau, et al. (2016) was used as the source for *A. mellifera's* tongue length.

The relationship between the degree of niche overlap and tongue length was tested using linear models. Model residuals were tested and deemed acceptable using the tests of dispersion and normality within the R package "DHARMa" (Hartig, 2022).

### 2.2.2.3 Niche overlap in relation to plant functional richness

Plant functional richness for each pasture was quantified based on two key functional traits: flower shape and colour. These traits were quantified using pictures of different species on Artdatabanken (SLU Artdatabanken, 2023). The flower colour assessment was done by ocular inspection in accordance with table A1, see Appendix.

The flower shape assessment was done in accordance with Launza et al. (2023)'s method for flower morphology; each plant species was divided into one of six different categories of flower shapes (figure 1); tube, papilionaceous, open, capitulum,

campanulate and brush. For species suspected to have either papilionaceous or capitulum flower shape, family affiliation was checked since all Fabaceae have papilionaceous shape and all Asteraceae have capitulum shape.
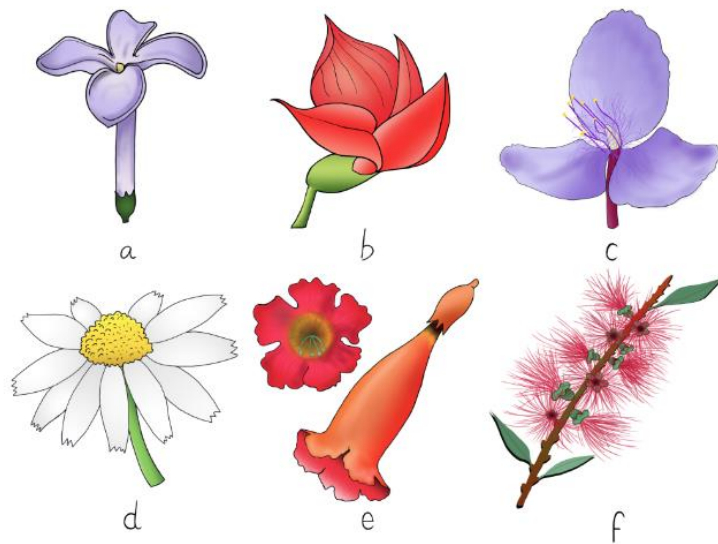


**Figure 1 Flower shapes**
The six different categories of flower shapes; tube (a), papilionaceous (b), open (c), capitulum (d), campanulate (e) and brush (f). *Image Source*: Launza et al., 2023. The authors have given their permission for usage of the image.

Plant functional richness (FRic) of each pasture was then quantified using flower shape and colour for each species and the flexible distance-based framework (dbFD) available in "Functional Diversity (FD)" R package (Laliberté et al., 2010). Specifically, as both traits were categorical, functional richness (FRic) was measured as the number of unique trait combinations within each pasture.

The relationship between the degree of niche overlap of each bumblebee species and plant functional richness were tested using linear models. Two models were specified, a model with individual slopes for each species or a model with a general slope for all species (i.e., niche overlap ~ bumblebee species + richness or niche overlap ~ bumblebee species * richness). Model selection to determine the best-fitting model was made using the Akaike information criterion. AIC differences of more than two, indicate that one model better describes the data (Burnham et al., 2004). Model residuals were tested and deemed acceptable using the tests of normality and dispersion within the R package "DHARMa" (Hartig, 2022).

# 3. Results

## 3.1 Diet breadth

The plant pollinator network illustrates the interactions between the different bee species and plant species (figure 2). *A. mellifera* and *B. terrestris* had the most interactions (n = 36 and 36 respectively), and largely overlaps in interaction (figure 2). The other bumblebee species also largely overlaps in interaction.
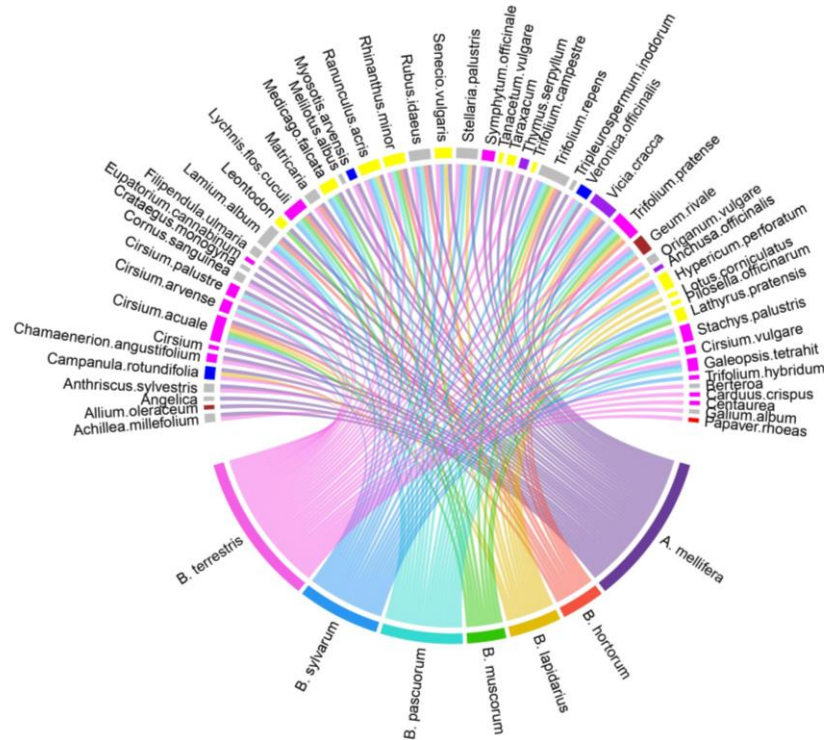


**Figure 2 Plant pollinator network**
Plant pollinator network depicting observed interactions between the different bee species (honeybee *A. mellifera* and bumblebee species (*Bombus* spp.)) and the different plant species. The width of each band from each bee species indicates the number of different plant species it was found to forage on. It does not take into account the frequency of foraging visits. The plants are presented with their flower colour, except for white flowers which are presented with grey.

*A. mellifera* and *B. terrestris* were found to forage on the highest number of plant species in semi-natural grasslands (Figure 3). They also foraged on significantly more plant species than the other five bumblebee species.

In total numbers of plant species each bee species interacted with, *A. mellifera* and *B. terrestris* had substantially wider diet breadth than the other bumblebee species (figure 3, left). However, plant richness varied greatly among sites for all species and for all bumblebee species except for *B. terrestris* it appears most common to have no interaction at a given site (figure 3, right).

The Tukey Honest Significant Difference (HSD) tests showed that bee species differed significantly in the number of different plant species they foraged on (figure 3, right, table A2 in Appendix). *A. mellifera* foraged on significantly more plant species than all species except *B. terrestris*. *B. terrestris* foraged on significantly more plant species than all species but *A. mellifer*a and *Bombus pascuorum*.

However, differences among species in diet breadth could be divided into three levels: wide diet breadth; *A. mellifera* and *B. terrestris*, intermediate diet breadth; *B. pascuorum* and *Bombus sylvarum*, and narrow diet breadth; *Bombus hortorum*, *Bombus lapidarius* and *B. muscorum*.
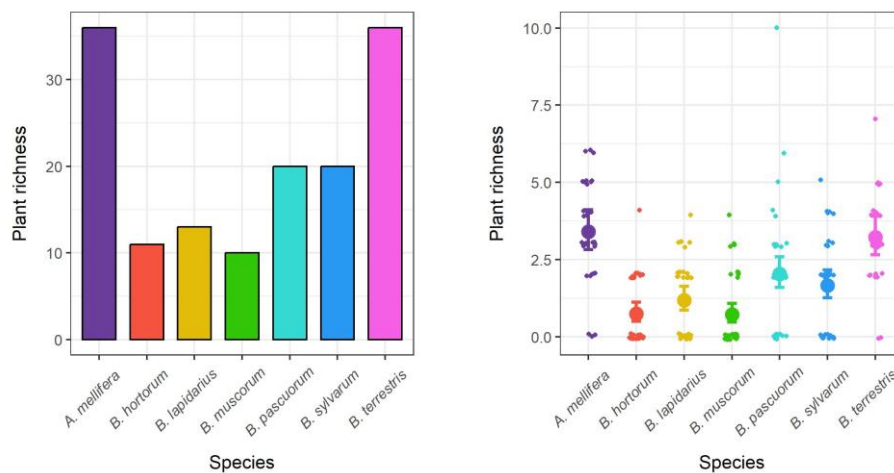


**Figure 3 Plant richness**
Number of different plant species each bee species foraged on (Plant richness), in total (left) and per site (right). On the right plot, large dots and whiskers indicate mean richness ± 95% confidence interval. Small dots indicate actual data.

## 3.2 Niche overlap in relation to bumblebee species

Bumblebee species differed in their degree of niche overlap with honeybees. *B. hortorum* was found to have the lowest niche overlap, having, on average, no significant niche overlap. *B. sylvarum* and *B. muscorum* showed an intermediate level of niche overlap with *A. mellifera* given that the mean niche overlap value was above 2, thereby significant, yet the lower 95% confidence interval fell below 2 (figure 4, table 1).

In contrast, *B. lapidarius*, *B. pascuorum* and *B. terrestris* all exhibited high and significant niche overlap with *A. mellifera*, as the 95% confidence intervals were well above 2 (figure 4, table 1).

Comparing the niche overlap among the bumblebee species, *B. hortorum* was found to have significantly lower niche overlap from *B. lapidarius* (diff = 3.379, p = 0.034), *B. pascuorum* (diff = 3.207, p = 0.040) and *B. terrestris* (diff = 3.617, p = 0.007) (figure 4). There were no significant differences in niche overlap among the remaining bumblebee species (all p values > 0.05) (table A3, in Appendix).
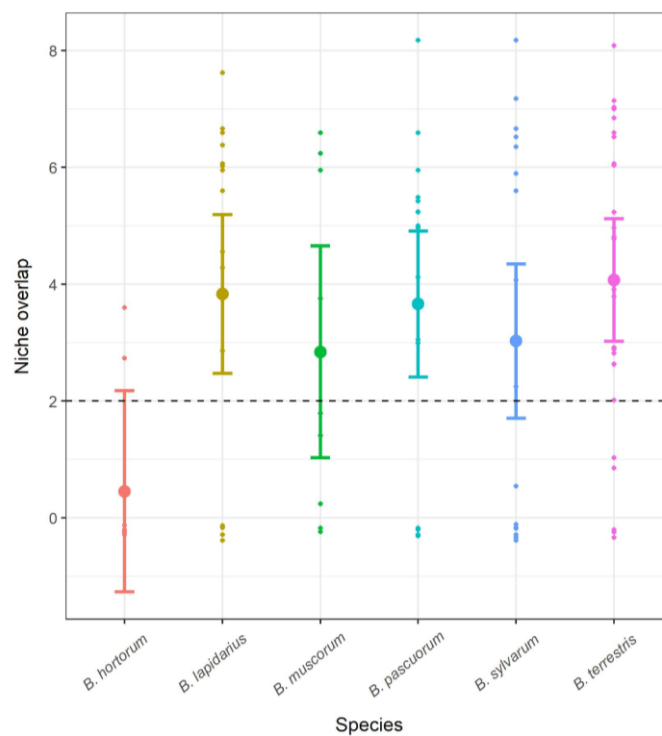


**Figure 4 Niche overlap between bumblebee species**
Niche overlap between honeybee and the different bumblebee species. The niche overlap at each site for each species (small dot) as well as the mean niche overlap for each species of bumblebee (big dot) is presented. The mean is presented with 95% confidence intervals bars. Niche overlap values above the dashed line at 2 are considered significant.

**Table 1:** Mean niche overlap for the different bumblebee species. The lower 95% and upper 95% confidence interval limits are also presented.

| Species | Mean niche overlap | Lower 95% confidence interval | Upper 95% confidence interval |
|---|---|---|---|
| *B. hortorum* | 0.451 | -1.270 | 2.172 |
| *B. lapidarius* | 3.830 | 2.469 | 5.190 |
| *B. muscorum* | 2.846 | 1.021 | 4.651 |
| *B. pascuorum* | 3.658 | 2.409 | 4.907 |
| *B. sylvarum* | 3.025 | 1.704 | 4.345 |
| *B. terrestris* | 4.068 | 3.020 | 5.116 |

## 3.3 Niche overlap in relation to tongue length

It was found that the degree of niche overlap with honeybees was structured by interspecific differences in bumblebee tongue length. Regression analysis revealed that the niche overlap between honeybees and bumblebees declined significantly with increasing tongue length of the bumblebee species ($t = -3.377$, $p = 0.001$, adjusted $R^2 = 0.097$) (figure 5).
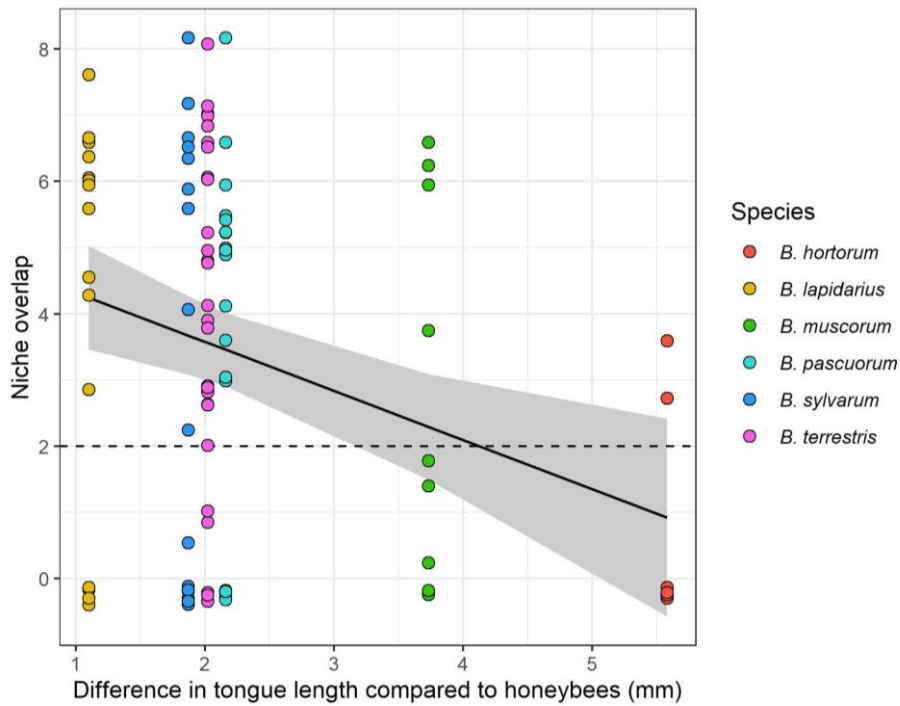


**Figure 5 Niche overlap in relation to tongue length**
Niche overlap between honeybee and the different bumblebee species in relation to tongue length (mm). The niche overlap is presented per site and the linear regression is presented with a 95% confidence interval (the light grey ribbon). Nich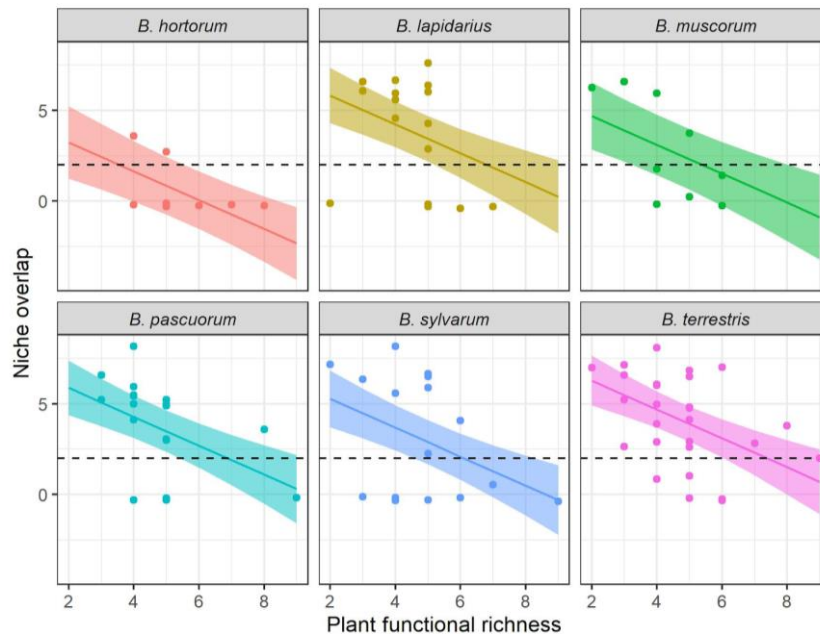e overlap values above the dashed line at 2 are significant. Line of best fit: Niche overlap = 5.062 - (0.742 * tongue length).

# 3.4 Niche overlap in relation to plant functional richness

Niche overlap was affected by the functional richness of the plant community within each grassland. Niche overlap between honeybees and bumblebees declined significantly with increasing plant functional richness for all bumblebee species (t = -4.450, p < 0.001) (figure 6). The Akaike Information Criterion (AIC) determined that the best fitting model was the one that included bumblebee species and plant functional richness, without an interaction (i.e., species differed in their intercept, but had the same slope (table 2) (ΔAIC: 8.277)). As such, the amount of plant functional richness required to reduce niche overlap with honeybees to insignificant levels differed between bumblebee species (i.e., the point at which the upper confidence interval falls below two) (figure 6).

   *B. hortorum* require the lowest amount of plant functional richness to reduce niche overlap with honeybees to insignificant levels, at value of around 5.5 (figure 6). After that follows in order *B. muscorum* (8), *B. sylvarum* (around 8.25), *B. pascuorum* (above 9), *B. lapidarius* (above 9) and lastly *B. terrestris* (above 9) (figure 6). Thus, there is insignificant levels of niche overlap between *B. terrestris* and *A. mellifera* only when plant functional richness exceeds a value of 9 (figure 6).



**Figure 6 Niche overlap in relation to plant functional richness**
Niche overlap between honeybee and the different bumblebee species in relation to plant functional richness. The niche overlap is presented per site and the linear regression is presented with a 95% confidence interval (the coloured ribbon). Niche overlap values above the dashed line at 2 are significant.

However, it is worth noting that the adjusted R-squared value is relatively low (0.242) and based on the 95% confidence interval, the model appears to fit the different bumblebee species to varying degrees.

| Species | Intercept | Intercept Std. Error | Slope | Slope Std. Error |
|---|---|---|---|---|
| *B. hortorum* | 4.831 | 1.261 | -0.796 | 0.179 |
| *B. lapidarius* | 7.413 | 1.019 | -0.796 | 0.179 |
| *B. muscorum* | 6.287 | 1.138 | -0.796 | 0.179 |
| *B. pascuorum* | 7.472 | 1.031 | -0.796 | 0.179 |
| *B. sylvarum* | 6.866 | 1.055 | -0.796 | 0.179 |
| *B. terrestris* | 7.873 | 0.981 | -0.796 | 0.179 |

# 4.  Discussion

Niche overlap between honeybees and bumblebees in semi-natural grasslands was found to be structured by species differences in tongue length, as well as the functional richness of the plant community on which they forage. Both honeybees and bumblebees were found to foraged on a large number of plant species in semi-natural grasslands, however, *A. mellifera* and *B. terrestris* had substantially wider diet breadth. Further, there was significant niche overlap between honeybees and bumblebees, ranging from low niche overlap (e.g., *B. hortorum*) to high niche overlap (e.g., *B. terrestris*). The results also showed that niche overlap was structured by bumblebee tongue length, likely reflecting different floral use among bumblebee species. Thereto it was found that niche overlap was structured by plant functional richness in each grassland, in particular bumblebee species' niche overlap with honeybees declined in grasslands with greater plant functional richness. The study's results suggest that niche overlap differs not only between bumblebee species, but also environments, suggesting that negative effects of competition are likely highly system-specific, and require tailored conservation efforts to overcome.

The results showed that there was significant niche overlap between honeybees and bumblebees in semi-natural grasslands. The results found that niche overlap was structured by tongue length, as increased tongue length compared to *A. mellifera* decreased the bumblebee species' niche overlap, indicating reduction in food resource competition. This finding is supported by Cappellari et al. (2022), who found that pollinator species with similar proboscis length to honeybees had the highest niche overlap. However, when studying tongue length in relation to competition in the future, structuring of niche overlap could be improved by accounting for intraspecific differences in tongue length. For example, Eggenberger et al. (2019) found differences in individuals of the same bumblebee species (*B. lapidarius* and *B. pascuorum*) in rural and urban environments, highlighting that tongue length can differ significantly within species. Preferences are affected by how well the bee species tongue length matches to the flower's morphology (Sponsler et al., 2022). For example, short tongued bumblebees such as *B. terrestris* prefer open flower morphologies, i.e., open and campanulate flowers, whereas long tongued bumblebees such as *B. hortorum* prefer more closed flower morphologies i.e., papilionaceous and tube flowers (Sponsler et al., 2022), which can lead to niche differentiation between bee species. Bees with longer tongues also tend to visit deeper flowers (Peat et al., 2005). Interestingly, Balfour et al. (2013) found that bumblebees with longer tongues than honeybees outcompeted

honeybees in patches of lavender, which have long corolla tube flowers, as the short tongue of the honeybee led to inefficient foraging. As such, long-tongued bumblebees are most likely able to avoid or overcome competition from honeybees through foraging on deep corolla tube flowers that honeybees forage inefficiently on, highlighting the importance of conserving such flower species.

This study found that short tongued bumblebees exhibit greater niche overlap with honeybees, which suggests that competition with honeybees pose a greater threat to these species. It also found the bumblebee species with the longest tongue - *B. hortorum* – to have the lowest niche overlap, the only species to not have significant niche overlap. Contrary to this, Goulson et al. (2005) found that most bumblebee species that are in decline are those with long tongues and specialised on Fabaceae, further depicting the complexity behind bumblebee losses and the importance of continuing investigation into its causes. However, *B. hortorum* is not in decline (Goulson et al., 2005), and the results of this study suggest that competition with managed *A. mellifera* is likely not of major concern for *B. hortorum*. Instead, habitat loss that reduces the availability of flower species with deep corollas associated with long tongued bumblebees are a more primary concern for decline of long tongued bumblebees (Goulson et al., 2005). Similarly, the results found that the red listed and declining *B. muscorum*, with the second longest tongue, only have moderate niche overlap with honeybees, suggesting other factors such as habitat loss to be more important in its decline (Darvill et al., 2006; Goulson et al., 2005; SLU Artdatabanken, 2020). This further testifies to the importance of conserving habitats with high floral diversity for bumblebee conservation. In conclusion, tongue length plays a crucial role in structuring bumblebees niche overlap with honeybees. However, as tongue length structures bee floral preferences assessing the structure of the plant community is also important.

The study found that niche overlap declined in areas of high plant functional richness, indicating that highly diverse habitats may reduce food resource competition between honeybees and bumblebees. Reduced niche overlap in diverse habitats may result from these habitats allowing co-existing species to differentiate in their niche, as a greater diversity of floral resources facilitates more available niches (Navarro-López & Fargallo, 2015). Similarly, Walter-Hellwig et al. (2006) found that long tongued bumblebees avoid competition from experimentally placed honeybees by shifting between plant species during foraging. The study's findings are also supported by Doublet et al. (2022) who found that niche overlap between honeybees and bumblebees was marginally reduced in areas of high flower species richness. Furthermore, Doublet et al. (2022) found that increased flower species richness increased bee abundance in early and late summer. The results indicate that increasing functional richness could be an important way to combat bumblebees being outcompeted by honeybees, as it likely has a mediating effect on niche overlap between wild and managed bees. Thereby, demonstrating that diverse plant communities need to be conserved or restored and confirming the importance of conserving biodiversity.

All bee species were found to visit a large number of plants in the different pastures. However, the diet breadth of each bee species varied largely. The results showed that *A. mellifera* and *B. terrestris* had the widest diet breadth, which may be because they were the most common species in the collected data. Their diet breadth could be a result of more of their niche being detected than the other species', rather than them having a much broader niche. *A. mellifera* and *B. terrestris* were likely most frequent as both species had nests experimentally placed within the pastures, with *A. mellifera* placed to simulate abundance during beekeeping. However, both *A. mellifera* and *B. terrestris* are considered generalists, making it reasonable they would have a broader niche (Cappellari et al., 2022; Dafni et al., 2010). The wide diet breadth of both *A. mellifera* and *B. terrestris* also makes them more prone to niche overlap. The figure over the plant pollinator network illustrates this, as *A. mellifera* and *B. terrestris* interactions with plants overlaps greatly both with the other bumblebee species, and with each other. Bees being found to like to forage on a large number of plants demonstrates that semi-natural grasslands, such as pastures, with their large number of floral resources are important habitats for bees (Öckinger et al., 2007) and therefore crucial to ongoing conservation of wild bees.

Food resource competition between honeybees and bumblebees is affected by more factors than the pollinator and plant traits investigated here. The study only examines a few of the several plant and pollinator traits that affect plant pollinator interactions, and therefore niche overlap and competition among pollinators. A flower's accessibility to pollinators is determined by plant traits such as flower shape, corolla length and nectar-tube depth, as well as pollinator traits such as proboscis (tongue) length (Cappellari et al., 2022; Junker et al., 2013). For example, Cappellari et al. (2022) found that niche overlap with honeybees was correlated with both proboscis length (more similar to honeybees), as demonstrated herein, and body size (larger). Furthermore, flower scent and flower colour affect the attractiveness of flowers to pollinators, by advertising for nectar and pollen (Cappellari et al., 2022; Rowe et al., 2020) and generally bees strongly prefer plants with flower traits that indicate high levels of resources (Rowe et al., 2020). For example, several studies have found bee visitation to be affected by the fact that visual flower traits can indicated quantity and/or quality of nectar and pollen resources (Rowe et al., 2020) and Fornoff et al. (2017) found nectar sugar concentration to increase pollinator visitation frequency. By including more pollinator and plant traits in future studies structing of niche overlap could be improved and thereby give more insight into the mechanisms behind competition between honeybees and bumblebees.

Food resource competition between honeybees and wild bees has also been found to differ due to season, with Ropars et al. (2022) finding competition to be strongest at the beginning of the season (February-April) and then decreasing in May. They suggested that one explanation for this trend was a wider diversity of floral resources later in the season (May). This indicates that competition between honeybees and wild bees can vary throughout the season in response to changes in floral resource

availability, and thereby suggests that the need for conservation efforts to vary during the season. Further, bumblebees have been found to forage not only in grasslands but also on mass-flowering crops (Lindström et al., 2018). Here the temporal effects are more substantial as agricultural resource areas only are available for a short period during the season, making other floral resources from e.g., semi-natural habitats essential (Persson & Smith, 2013). Herbertsson et al. (2016) findings further testify to this. They found that the surrounding environment impact honeybees' impact on bumblebees, as bumblebee densities declined in homogeneous landscapes after adding honeybees but did not decline in heterogeneous landscapes. Herbertsson et al. (2016) argues that this indicates that competition occurs when food resources supplied by semi-natural areas are scarce and that heterogeneity, i.e., high levels of semi-natural grasslands, can mitigate competition. In summary, this shows the importance of examining competition between honeybees and bumblebees not only on a small-scale, investigating plant and pollinator traits, but also on a larger scale, having both a landscape perspective and accounting for temporal effects, to gain a more comprehensive assessment of the impacts.

The results are probably affected by abundance of honeybees varying among sites, as the sites were at different distances from the placed honeybee beehives. This would result in different levels of honeybee foraging activity at the different sites, therefore influencing competition. Similarly, Ropars et al. (2022) suggest that the removal of beehives could explain the detected lower competition for food resource between wild bees and honeybees later in the season. As when the beehives were removed, the visitation rates of honeybees decreased (Ropars et al., 2022). Studies have found bees near beehives to suffer several negative effects. Goulson and Sparrow (2009) found all investigate bumblebee species to be smaller in areas with honeybees and suggested consequences for colony success. Concordantly, Thomson (2004) found that bumblebee colonies near introduced honeybees had impaired foraging which contributed to reduced reproductive success. Thereto, Linström et al. (2016) found that bumblebee densities decreased when honeybees were added. Thus, from a conservation perspective, it is important that the placement of apiaries is done in such a way to avoid conservation areas or those with rare bumblebee species, to mitigate the negative effects of competition.

All in all, competition from honeybees poses a threat to bumblebee diversity and survival. This is an issue to mankind beyond the existential tragedy of potential species declines for two main reasons. First, losses of biodiversity make ecosystems more fragile in relation to climate change (Kühsel & Blüthgen, 2015). Secondly, Page et al. (2021) found honeybees to be substantially less effective pollinators than both above effective and average effective bee pollinators, such as bumblebees, which are crucial pollinators through their ability of buzz pollination (Cooley et al., 2021). Thereby honeybees outcompeting bumblebees poses a threat to both crops and wild plants' reproduction successes. It also poses the risk of a cascading effect to both bumblebee and plant biodiversity. Honeybees are often placed in the environment to help

pollinate crops, as well as produce honey products. The benefit of these agricultural services should however be weighed against the costs of the numerous negative effects honeybees has on wild bees, underscoring a need to improve the management. For example, the competition from honeybees could be mitigated by keeping honeybee densities low to limit resource depletion, thereby ensuring sufficient floral resources for other bees. Furthermore, placement of apiaries should avoid conservation areas. Thereto, the results indicates that areas with high plant functional richness could mitigate competition, suggesting such areas could support apiaries without negatively affecting the wild bee community. Lastly, the results also suggest increasing the plant functional richness of areas where beehives are placed could help mitigate competition. Given ongoing bumblebee declines, further understanding the of underlying mechanisms are needed. This study illustrates the importance of preserving plant functional richness for reducing niche overlap, but to further understand bumblebee losses, future studies should assess how plant functional richness relates to bumblebee population dynamics (i.e., interannual trends). Furthermore, studies including more plant and pollinator traits would contribute to a more comprehensive understanding of niche overlap structures.

# 5.  Conclusions

This study shows that honeybees affect bumblebees through competition for food resources, here demonstrated by niche overlap. The results showed that bumblebees with similar tongue length to honeybee are most at risk of competition. Furthermore, the result that both tongue length and plant functional richness affects structure of niche overlap, indicates that the negative effects from competition from honeybees are highly system-specific, making customized conservation efforts essential for overcoming the effects. However, this study shows that no matter bumblebee species, competition, through decreased niche overlap, decreases with increasing plant functional richness. Thereby indicating that functional richness could be an important tool in combating bumblebees being outcompeted by honeybees and underscoring the importance of conserving areas with high plant functional richness such as semi-natural grasslands, to protect biodiversity.

# Acknowledgement

First, I would like to thank my supervisor Liam Kendall for all feedback and valuable suggestions, and all help with R. I would also like to thank the supervisor of the group supervision and my group for their important input on my thesis. Lastly, I want to thank friends and family for their help and support.

# References

Arbetman, M. P., Gleiser, G., Morales, C. L., Williams, P., & Aizen, M. A. (2017). Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20170204. https://doi.org/10.1098/rspb.2017.0204

B. Lanuza, J., Rader, R., Stavert, J., Kendall, L. K., Saunders, M. E., & Bartomeus, I. (2023). Covariation among reproductive traits in flowering plants shapes their interactions with pollinators. *Functional Ecology*. https://doi.org/10.1111/1365-2435.14340

Balfour, N. J., Garbuzov, M., & Ratnieks, F. L. (2013). Longer tongues and swifter handling: why do more bumble bees (Bombus spp.) than honey bees (Apis mellifera) forage on lavender (Lavandula spp.)?. *Ecological entomology*, *38*(4), 323-329. https://doi.org/10.1111/een.12019

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological methods & research*, *33*(2), 261-304. DOI: 10.1177/0049124104268644

Cane, J. H., & Tepedino, V. J. (2017). Gauging the effect of honey bee pollen collection on native bee communities. *Conservation Letters*, *10*(2), 205-210. https://doi.org/10.1111/conl.12263

Cappellari, A., Bonaldi, G., Mei, M., Paniccia, D., Cerretti, P., & Marini, L. (2022). Functional traits of plants and pollinators explain resource overlap between honeybees and wild pollinators. *Oecologia*, *198*(4), 1019-1029. https://doi.org/10.1007/s00442-022-05151-6

Cariveau, D. P., Nayak, G. K., Bartomeus, I., Zientek, J., Ascher, J. S., Gibbs, J., & Winfree, R. (2016). The allometry of bee proboscis length and its uses in ecology. *PloS one*, *11*(3), e0151482. https://doi.org/10.1371/journal.pone.0151482

Cooley, H., & Vallejo-Marín, M. (2021). Buzz-pollinated crops: a global review and meta-analysis of the effects of supplemental bee pollination in tomato. *Journal of Economic Entomology*, *114*(2), 505-519. https://doi.org/10.1093/jee/toab009

Dafni, A., Kevan, P., Gross, C. L., & Goka, K. (2010). Bombus terrestris, pollinator, invasive and pest: An assessment of problems associated with its widespread introductions for commercial purposes. *Applied Entomology and Zoology*, *45*(1), 101-113. https://doi.org/10.1303/aez.2010.101

Darvill, B., Ellis, J. S., Lye, G. C., & Goulson, D. (2006). Population structure and inbreeding in a rare and declining bumblebee, Bombus muscorum (Hymenoptera: Apidae). *Molecular Ecology*, *15*(3), 601-611. https://doi.org/10.1111/j.1365-294X.2006.02797.x

De Luca, P. A., & Vallejo-Marin, M. (2013). What's the 'buzz'about? The ecology and evolutionary significance of buzz-pollination. *Current opinion in plant biology*, *16*(4), 429-435. https://doi.org/10.1016/j.pbi.2013.05.002

Doublet, V., Doyle, T., Refoy, I., Hedges, S., Carvell, C., Brown, M. J., & Wilfert, L. (2022). Increasing flower species richness in agricultural landscapes alters insect pollinator networks: Implications for bee health and competition. *Ecology and Evolution*, *12*(10), e9442. https://doi.org/10.1002/ece3.9442

Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., & Moretti, M. (2019). Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *Journal of Animal Ecology*, *88*(10), 1522-1533. https://doi.org/10.1111/1365-2656.13051

Elliott, B., Wilson, R., Shapcott, A., Keller, A., Newis, R., Cannizzaro, C., Burwell, C., Smith, T., Leonhardt, S.D., Kaemper, W. and Wallace, H.M. (2021). Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic and Applied Ecology*, *50*, 169-180. https://doi.org/10.1016/j.baae.2020.12.002

Fornoff, F., Klein, A. M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H. M., & Ebeling, A. (2017). Functional flower traits and their diversity drive pollinator visitation. *Oikos*, *126*(7), 1020-1030. https://doi.org/10.1111/oik.03869

Gotelli, N. J., & Graves, G. R. (1996). *Null Models in Ecology*. Smithsonian Institution Press, Washington, D.C.

Gotelli, N. J., Hart, E. M., & Ellison, A. M. (2015) EcoSimR: Null model analysis for ecological data. R package version 0.1.0. http://github.com/gotellilab/EcoSimR DOI: 10.5281/zenodo.16522

Goulson, D. (2003). Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 1-26. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Goulson, D., Hanley, M. E., Darvill, B., Ellis, J. S., & Knight, M. E. (2005). Causes of rarity in bumblebees. *Biological conservation*, *122*(1), 1-8. https://doi.org/10.1016/j.biocon.2004.06.017

Goulson, D., & Sparrow, K. R. (2009). Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of insect conservation*, *13*, 177-181. https://doi.org/10.1007/s10841-008-9140-y

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957. DOI: 10.1126/science.1255957

Hardin, G. (1960). The Competitive Exclusion Principle: An idea that took a century to be born has implications in ecology, economics, and genetics. *science*, *131*(3409), 1292-1297. DOI: 10.1126/science.131.3409.1292

Harmon-Threatt, A. N., & Ackerly, D. D. (2013). Filtering across spatial scales: phylogeny, biogeography and community structure in bumble bees. *PLoS One*, *8*(3), e60446. https://doi.org/10.1371/journal.pone.0060446

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models_. R package version 0.4.6, https://CRAN.R-project.org/package=DHARMa

Herbertsson, L., Lindström, S. A., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic and Applied Ecology*, *17*(7), 609-616. https://doi.org/10.1016/j.baae.2016.05.001

Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H., & Stang, M. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional ecology*, *27*(2), 329-341. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2435.12005

Kendall, L., Bernhardsson, O., & Smith, H. G. (2022, juli*). Konkurrens mellan vilda bin och honungsbin – fördjupande fältförsök 2022: Delrapport – juli 2022*. Centrum för miljö- och klimatvetenskap, Lunds universitet.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, *274*(1608), 303-313. https://doi.org/10.1098/rspb.2006.3721

Kühsel, S., & Blüthgen, N. (2015). High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. *Nature communications*, *6*(1), 7989. https://doi.org/10.1038/ncomms8989

Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299-305. Laliberté, E., Legendre, P., and B. Shipley. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.1.

Lindström, S. A., Herbertsson, L., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proceedings of the Royal Society B: Biological Sciences, 283(1843), 20161641. https://doi.org/10.1098/rspb.2016.1641

Lindström, S. A., Klatt, B. K., Smith, H. G., & Bommarco, R. (2018). Crop management affects pollinator attractiveness and visitation in oilseed rape. *Basic and Applied Ecology*, *26*, 82-88. https://doi.org/10.1016/j.baae.2017.09.005

Navarro-Lopez, J., & Fargallo, J. A. (2015). Trophic niche in a raptor species: the relationship between diet diversity, habitat diversity and territory quality. *PLoS One*, *10*(6), e0128855. https://doi.org/10.1371/journal.pone.0128855

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, *120*(3), 321-326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Page, M.L., Nicholson, C.C., Brennan, R.M., Britzman, A.T., Greer, J., Hemberger, J., Kahl, H., Müller, U., Peng, Y., Rosenberger, N.M. and Stuligross, C. (2021). A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. *American Journal of Botany*, *108*(11), 2196-2207. https://doi.org/10.1002/ajb2.1764

Page, M. L., & Williams, N. M. (2023). Honey bee introductions displace native bees and decrease pollination of a native wildflower. *Ecology*, *104*(2), e3939. https://doi.org/10.1002/ecy.3939

Peat, J., Tucker, J., & Goulson, D. (2005). Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers?. *Ecological Entomology*, *30*(2), 176-181. https://doi.org/10.1111/j.0307-6946.2005.00676.x

Persson, A. S., & Smith, H. G. (2013). Seasonal persistence of bumblebee populations is affected by landscape context. *Agriculture, ecosystems & environment*, *165*, 201-209. https://doi.org/10.1016/j.agee.2012.12.008

Persson, A. S., Rundlöf, M., Clough, Y., & Smith, H. G. (2015). Bumble bees show trait-dependent vulnerability to landscape simplification. *Biodiversity and Conservation*, *24*, 3469-3489. https://doi.org/10.1007/s10531-015-1008-3

Pianka, E. R. (1973). The structure of lizard communities. *Annual review of ecology and systematics*, *4*(1), 53-74.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raderschall, C. A., Bommarco, R., Lindström, S. A., & Lundin, O. (2021). Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. *Agriculture, Ecosystems & Environment*, *306*, 107189. https://doi.org/10.1016/j.agee.2020.107189

Rasmussen, C., Dupont, Y.L., Madsen, H.B., Bogusch, P., Goulson, D., Herbertsson, L., Maia, K.P., Nielsen, A., Olesen, J.M., Potts, S.G. and Roberts, S.P. (2021). Evaluating competition for forage plants between honey bees and wild bees in Denmark. *Plos one*, *16*(4), e0250056. https://doi.org/10.1371/journal.pone.0250056

Ropars, L., Affre, L., Thébault, É., & Geslin, B. (2022). Seasonal dynamics of competition between honey bees and wild bees in a protected Mediterranean scrubland. *Oikos*, *2022*(4), e08915. https://doi.org/10.1111/oik.08915

Rowe, L., Gibson, D., Bahlai, C. A., Gibbs, J., Landis, D. A., & Isaacs, R. (2020). Flower traits associated with the visitation patterns of bees. *Oecologia*, *193*, 511-522. https://doi.org/10.1007/s00442-020-04674-0

SLU Artdatabanken. (2020). *Rödlista 2020 - övergripande delar*. Uppsala: SLU Artdatabanken.

SLU Artdatabanken. (2023). Artfakta. https://artfakta.se/artinformation (Hämtad April 2023)

Sponsler, D., Kallnik, K., Requier, F., Classen, A., Maihoff, A. F., Sieger, J., & Steffan-Dewenter, I. (2022). Floral preferences of mountain bumble bees are constrained by functional traits but flexible through elevation and season. *Oikos*, *2022*(3), e08902. https://doi.org/10.1111/oik.08902

Steffan-Dewenter, I., & Tscharntke, T. (2000). Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia*, 288-296. https://www.jstor.org/stable/4222543

Thomson, D. (2004). Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology*, *85*(2), 458-470. https://doi.org/10.1890/02-0626

Ulrich, W., & Gotelli, N. J. (2007). Null model analysis of species nestedness patterns. *Ecology*, *88*(7), 1824-1831. https://doi.org/10.1890/06-1208.1

Walther-Hellwig, K., Fokul, G., Frankl, R., Büchler, R., Ekschmitt, K., & Wolters, V. (2006). Increased density of honeybee colonies affects foraging bumblebees. *Apidologie*, *37*(5), 517-532. https://doi.org/10.1051/apido:200701

Whittaker, R. H., Levin, S. A., & Root, R. B. (1973). Niche, habitat, and ecotope. *The American Naturalist*, *107*(955), 321-338. https://doi.org/10.1086/282837

Williams, P. H., & Osborne, J. L. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie*, *40*(3), 367-387. https://doi.org/10.1051/apido/2009025

Wood, T.J., Ghisbain, G., Rasmont, P., Kleijn, D., Raemakers, I., Praz, C., Killewald, M., Gibbs, J., Bobiwash, K., Boustani, M. and Martinet, B. (2021). Global patterns in bumble bee pollen collection show phylogenetic conservation of diet. *Journal of Animal Ecology*, *90*(10), 2421-2430. https://doi.org/10.1111/1365-2656.13553

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of applied ecology*, *44*(1), 50-59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

# Appendix

Table A1: Description of flower colour assessment, and how observed flower colour was grouped.

| Flower colour observed | Flower colour noted |
|---|---|
| **White** | White |
| **Yellow** | Yellow |
| **Red** | Red |
| **Light pink - magenta** | Magenta |
| **Dark magenta - indigo** | Purple |
| **Indigo - light blue** | Blue |
| **Majority of flower is brown, or beige** | Brown |

Table A2: Pairwise comparison of mean diet breadth (plant richness) between bee species.

| Compared species | Estimate | Standard Error | Z-ratio | P-value |
|---|---|---|---|---|
| *A. mellifera - B. hortorum* | 1.817 | 0.299 | 6.076 | <.001 |
| *A. mellifera - B. lapidarius* | 1.291 | 0.241 | 5.363 | <.001 |
| *A. mellifera - B. muscorum* | 1.743 | 0.290 | 6.016 | <.001 |
| *A. mellifera - B. pascuorum* | 0.575 | 0.186 | 3.088 | 0.033 |
| *A. mellifera - B. sylvarum* | 0.856 | 0.205 | 4.180 | 0.001 |
| *A. mellifera - B. terrestris* | 0.092 | 0.162 | 0.566 | 0.998 |
| *B. hortorum - B. lapidarius* | -0.526 | 0.350 | -1.504 | 0.743 |
| *B. hortorum - B. muscorum* | -0.074 | 0.385 | -0.192 | 1.000 |
| *B. hortorum - B. pascuorum* | -1.242 | 0.315 | -3.944 | 0.002 |
| *B. hortorum - B. sylvarum* | -0.961 | 0.326 | -2.948 | 0.050 |
| *B. hortorum - B. terrestris* | -1.726 | 0.301 | -5.732 | <.001 |
| *B. lapidarius - B. muscorum* | 0.452 | 0.342 | 1.322 | 0.842 |
| *B. lapidarius - B. pascuorum* | -0.716 | 0.260 | -2.751 | 0.086 |
| *B. lapidarius - B. sylvarum* | -0.435 | 0.274 | -1.591 | 0.688 |
| *B. lapidarius - B. terrestris* | -1.199 | 0.243 | -4.932 | <.001 |

| | | | | |
|---|---|---|---|---|
| *B. muscorum - B. pascuorum* | -1.168 | 0.306 | -3.815 | 0.003 |
| *B. muscorum - B. sylvarum* | -0.887 | 0.318 | -2.794 | 0.077 |
| *B. muscorum - B. terrestris* | -1.651 | 0.292 | -5.660 | <.001 |
| *B. pascuorum - B. sylvarum* | 0.280 | 0.227 | 1.234 | 0.881 |
| *B. pascuorum - B. terrestris* | -0.484 | 0.190 | -2.553 | 0.141 |
| *B. sylvarum - B. terrestris* | -0.764 | 0.208 | -3.680 | 0.004 |

Table A3: Pairwise comparison of mean niche overlap with honeybees between bumblebee species.

| Compared species | Difference in niche overlap | P-value |
|---|---|---|
| *B. lapidarius - B. hortorum* | 3.379 | 0.034 |
| *B. muscorum - B. hortorum* | 2.386 | 0.412 |
| *B. pascuorum - B. hortorum* | 3.207 | 0.040 |
| *B. sylvarum - B. hortorum* | 2.574 | 0.183 |
| *B. terrestris - B. hortorum* | 3.617 | 0.007 |
| *B. muscorum - B. lapidarius* | -0.993 | 0.953 |
| *B. pascuorum - B. lapidarius* | -0.172 | 1.000 |
| *B. sylvarum - B. lapidarius* | -0.805 | 0.959 |
| *B. terrestris - B. lapidarius* | 0.238 | 1.000 |
| *B. pascuorum - B. muscorum* | 0.821 | 0.976 |
| *B. sylvarum - B. muscorum* | 0.188 | 1.000 |
| *B. terrestris - B. muscorum* | 1.231 | 0.851 |
| *B. sylvarum - B. pascuorum* | -0.633 | 0.982 |
| *B. terrestris - B. pascuorum* | 0.410 | 0.996 |
| *B. terrestris - B. sylvarum* | 1.043 | 0.821 |