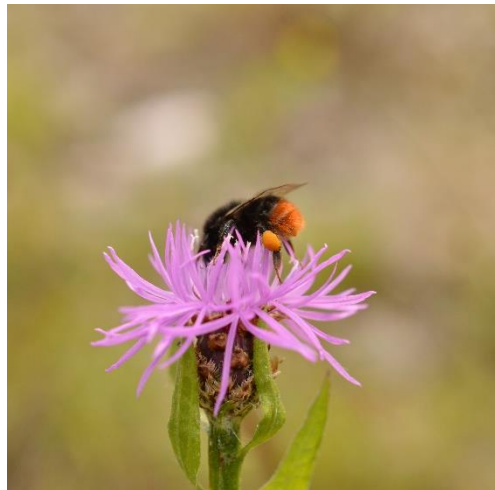# Dependence of wild bee communities and their ecological and functional traits on quality and quantity of habitat resources

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[1] Für alle weiteren Personen die an der Betreuung beteiligt waren siehe S.17.

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Dependence of wild bee communities and their ecological and functional traits on quality and quantity of habitat resources

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Abstract

Wild bees are exposed to species decline on a wide scale. As they depend on species- specific habitat requirements, the loss and dissociation of foraging and nesting habitats represents one of the greatest threats to them. Furthermore, high honeybee densities can lead to competition on foraging resources. To analyse the community structure of wild bees and their dependence on habitat resources, we set up pan traps in 14 study areas in the Inn valley (Austria). Two groups of sites were distinguished, differing in their form of cultivation and habitat structure. (1) RS-EF sites are characterised as richly structured and extensively farmed sites; (2) PS-IF sites show a low degree of landscape elements, but high flower abundance and are located in an intensively farmed environment. In order to assess resource availability, the immediate surrounding of pan traps was analysed through aerial photo analysis using ArcGis Pro and drone images (DJI Mini II).

We determined 117 wild bee species at 1988 individuals as well as 2631 honeybees (*Apis melifera).* Species abundance and richness correlated positively with increasing habitat structures like ecotone length of trees and bushes and blue flower colours. On the other hand, bees' biomass correlated with open field areas with a higher share of flower abundance. Our results indicate that environmental parameters affect functional traits, as we found differences in structure and traits of wild bee communities between both groups of sites. On (1) RS-EF sites, proportionately more polylectic, social, below-ground as well as above-ground nesting, female bees were collected featuring a lower average of biomass. Secondly, the wild bees' community on (2) PS-IF sites was mainly characterised by proportionately more oligolectic, solitary, parasitic and male bees featuring a higher average of biomass.

Our findings underline the direct impact of a dense landscape matrix on bees' communities. We suppose that landscape structures that provide high-quality resources and connect habitats enhance species abundance, richness, and a wide variety of species traits. What's more, honeybee hives should not be located near species-rich habitats in order to avoid negative competition impact.

1 Introduction

Land management and settlement construction have been major drivers of landscape change in the last decades (Schwick et al. 2010). In agriculturally used land, this change manifests itself in the increase of intensive land farming and the fallowing of areas that are no longer economically viable (Lachat et al. 2010). The resulting loss of diversely-structured areas represents a threat for insect populations worldwide and reduces their abundance and species richness (Foley et al. 2005; Kremen et al. 2002).

Bees are important protagonists in grassland ecosystems and are considered as most efficient pollinators. Thus, maintaining stable wild-bee populations is crucial for, among others, food safety worldwide (Klein et al. 2007). In Austria, there are 702 known species, of which 400 species have been documented in the state of Tyrol (34 of these species still unpublished or with need of review) (Gusenleitner et al. 2012; Lanner et al. 2020; Zettel and Wiesbauer 2014; Kopf unpublished 09-03-22). The broad variety of wild-bee species translates into a multitude of different specialisations and life-history traits, such as nesting and social types as well as pollen-collection behaviour.

Wild bees' habitats must comply with three main requirements. In addition to adequate nesting grounds and species-specific pollen resources, building material for nesting must be available. These resources need to be provided in adequate quality and quantity within the wild bees' foraging distances (Westrich 2018). These dependencies as well as low reproduction rates can present crucial disadvantages in changing environmental conditions (Zurbuchen and Müller 2012). Thus, well-structured landscapes as well as flowering abundance and composition allow for the highest bee diversity (Knop et al. 2006; Potts et al. 2003; Steffan-Dewenter et al. 2002). One of the structure-defining parameters are supposed to be ecotones. These transitional areas between two ecosystems can provide important resources for pollinators and are known to enhance total biodiversity (Duelli 1997; Martin et al. 2019). Hedgerows and forest edges adjacent to open fields can offer nesting sites and diverse herbaceous margins for pollen collection (Kells and Goulson 2003). Furthermore, the availability of margins of arable fields and wildflower strips lead to higher species richness and abundance (Carvell et al. 2007; Ganser et al. 2021).

The impoverishment of structures in agricultural landscapes is likely to increasingly disassociate foraging and nesting habitats (Zurbuchen and Müller 2012). As foraging distances of wild-bee species are species-specifically limited (Zurbuchen et al. 2010b), the loss or disassociation of nesting and foraging structures can lead to a decline or even regional extinction of wild-bee populations (Zurbuchen and Müller 2012). Reinforced by further causes of risk, this leads to an alarming number of wild bee species listed as endangered or extinct on the Red List of Switzerland (45%) and Germany (49%) (Amiet 1994; Westrich et al. 2011, currently no Red List available for Austria).

Another potential driver for the decline of pollinator richness and abundance may be the rising honeybee abundance. In the year 2020, the Austrian number of hives, registered by the beekeeping association (Biene Österreich- Imkereidachverband), increased to 426,121 hives (Boigenzahn et al. 2021). The increasing trend of honeybee hives and decreasing food resources can lead to harmful competition for pollen and nectar. We expect competition between *Apis mellifera* and native bees, if flower resources are not distributed equally or not available in sufficient quality and quantity. Hence, in monotonous and intensively managed landscapes, the overlapping requirement of food resources between *Apis mellifera* and other pollinators is supposed to be another important driver of pollinator species decline (Zurbuchen and Müller 2012).

The objective of this study is to investigate the species composition of wild-bee communities and their distribution on grassland ecosystems in Tyrol (Austria) depending on selected environmental parameters. We defined two groups of sites that differ in their type of cultivation, exposure, and structure diversity. In detail, we focused on the following three research questions:

i) Which of the parameters habitat structure and flower-colour abundance have an impact on the abundance, biomass, and species richness of wild bees and to what extent?

We hypothesized that heterogenous habitat structures provide diverse supply of nesting and foraging resources and therefore enhance wild bees' abundance and species richness. Moreover, the abundance of tiny bee species is likely to increase with habitat structures as they are less mobile (Zurbuchen et al. 2010b). With respect to foraging resources, we assume that sites with a higher share of flowers also increase wild bees' abundance and diversity. High total flower abundance is hypothesized to correlate particularly with an increasing number of larger wild bee species. This hypothesis is based on the assumption that large flower clusters attract bees from further distances and enough food resources to prevent smaller offspring (Bosch 2008; Peterson and Roitberg 2006a). Summing up, well-structured sites are expected to serve as nesting and foraging habitats and poorly structured landscapes with high flowering abundance are assumed to serve predominantly as foraging habitats.

ii) Which parameters explain the distribution of the functional and ecological wild-bee traits pollen collecting, nesting type, social behaviour, and sex over the sites?

We expected complexity of habitats to influence species guilds due to their individual dependencies. On one hand, compositional heterogeneity of landscapes is associated with social-bee richness and is negatively related to below-ground nesting species. On the other hand, intensity of land management and increasing crop production can lead to a decrease of above-ground nesting bees and solitary species (Da Coutinho et al. 2018). Therefore, we expect higher numbers of social, solitary and above- ground nesting species on well-structured and below-ground nesting types in less diversely structured sites. In contrast, flower abundance and -colours are supposed to have an impact on pollen collection behaviour and to allow for the naturally occurring surplus production of female individuals, as female offspring requires sufficient food availability (Bosch 2008).

iii) How does the number of honeybees compare with the number of wild bees?

A correlation between honeybees and wild bees can theoretically go in both directions. A positive correlation would indicate the dependency of both bees on the same foraging resources. However, the more likely finding would be a negative correlation due to interspecific competition on food resources (Renner et al. 2021).

2   Material and methods

2.1   Experimental sites

The study was conducted in Tyrol, Austria, in the Inn valley between the cities of Innsbruck and Imst. Fourteen sites, which can be classified into two different management types and can be ordered along a gradient of heterogeneity of structures and flower colours, were selected. Half of the sites are located in the Natura 2000 protected area (Ortolan- Vorkommen Silz - Haiming - Stams). These seven sites are situated in an intensive land farming environment, over which some extensively managed meadows are scattered. The surrounding areas form a mosaic of various cultivations with quite small field sizes but a low degree of structuring elements like trees and bushes. The extensively managed meadows ("PS-IF") are mowed twice a year and dispose of a flowering strip, mowed only once a year, in August. The other half of sites were chosen for comparison and show a higher number on seminatural habitats than sites in the Natura 2000 area. These sites are characterised by an extensive management, mostly because of unfavourable farming conditions due to hillsides, wetlands, or recreational use. Because of their well-structured environment and heterogeneity in flowering plants, these sites were expected to host a broad variety of wild bee species and in the following described as "RS-EF" (see Supplement 1 & 2).

2.2   Bees' records

Following Potts et al. (2021), the bees were collected in pan traps. Each pan trap was composed of three differently coloured bowls with a filling capacity of 800 ml, the inside either yellow, blue, or white, the outside always green to avoid bee attraction from long distances. The group of bowls were raised on average height of the surrounding vegetation and mounted on a 120 cm long wooden stick. On each site, three pan traps (with each tree bowls) were positioned with a minimum of 15 m distance between them. In total, 126 traps were installed on 14 sites. During the sampling period, which began in mid-April 2021 and ended in mid-June 2021, pan traps were filled with salty water and odourless detergent to break surface tension. On average, every 10.125 days (± 2.976; min. 6 due to mowing actions; max. 17 due to bad weather conditions), the pan traps were emptied and refilled. In total, eight collection periods were conducted. Due to removal of pan traps by unknown persons, data for Site 5 in collection Period 1 are lacking.

2.3   Detecting flower colours

Sunny and calm weather was critical for drone flights conducted on the sampling days. Drone flights were carried out with the purpose to assess available flower colours to analyse the immediate environmental context of the pan traps. We shot pictures from 10 m to 50 m distance, orthogonal to the mid pan trap with a mini drone of the type DJI Mini 2. To minimize the impact of variation in brightness conditions, the pictures were taken between 09:00 am and 15:30 pm. Each drone picture (10 m drone flight hight) covered approximately 385 m² of the immediate surrounding of the pan traps.

Pictures of drone flights were converted from DNG to TIFF- format and analysed using a python script, created in Anaconda Navigator 2.1.1 (Anon 2020). Threshold values for each colour (white, yellow, and blue) were determined in the python script and applicated on each picture to filter specific flower colours (see Supplement 3). However, only pictures from 10 m and 20 m flying hight were used since the pictures taken from greater heights were too low in resolution. Finally, a standard value of 0.001% and 0.002% for 10 and 20 m heights, respectively, representing the area covered by the coloured pan traps, was subtracted.

2.4   Determining species and biomass

The collected bees were sorted, counted, washed with water, labelled, and stored in a 70% ethanol solution. Other taxa and honeybees were transferred to the Tyrolian Museum of Nature (Tiroler Landesmuseum, Ferdinandeum Innsbruck). Wild bee specimens were identified to species level, using several keys: Amiet et al. 1996; Amiet et al. 1999; Amiet et al. 2001, 2004; Amiet et al. 2007, 2010; Dathe et al. 2016; Scheuchl 2000, 2006; and Schmid-Egger and Scheuchl 1996. Species names were adjusted by comparing with the accepted status provided by the Catalogue of Life (Bánki et al. 2022). The few individuals (15) that could not be identified by morphological characteristics were sent to the National Museum of Natural History, Luxembourg for DNA sequencing.

For every bee species, several life-history and ecological traits were recorded to categorise wild-bee communities, based on information provided by Westrich (2018). The variables chosen were pollen specialisation (polylectic, oligolectic), nesting behaviour (below-ground, above-ground), sociality (social, solitary, parasite, communal), and sex/caste (male, female / queen, worker where applicable). This dataset allowed us to better understand assemblages and combinations of functional diversity traits of bees in different environments.

In a next step, ten individuals per species and sex (or fewer, depending on the availability in the catch) were pinned to measure the intertegular distance (ITD). This measure is known to correlate strongly with biomass (Kendall et al. 2019) and provides a good proxy of body size (Cane 1987). The ITD was measured using a macroscope with apochromatic zoom system and digital calliper (Leica Z6Apo). Most species did not reach the mark of ten individuals and fewer individuals were measured. Furthermore, for bumblebees, queens, males, and workers were distinguished, as they differ significantly in size. Average size and biomass were calculated for each species following Cane (1987).

2.5   Heterogeneity of structures

To gain information about the structure and patchiness of the environment, ArcGIS Pro (2.7.0) was used to digitise the surrounding of the pan traps. Based on orthophotos with a resolution of 20 cm, provided by the Tyrolian government (Land Tirol - data.gv.at), the focus lay on the area within 150 m, representing 79654 m² of surrounding area of the pan traps. Inside this ambit, every small-scale structure such as boundary ridges, waysides, brook sides, but also borders of houses, gardens and power poles were digitised. For single trees, bushes, hedgerows, and woods, the treetop coverage was used since we expected the treetop to have a stronger impact than the trunk on the micro-environmental scale. Between these polygons of homogenous structure, it was ensured to leave no gaps or overlaps. This made it possible to subtract the perimeter of the 150 m radius from the sum of perimeters of all polygons and then divide by two. The sum of perimeters for every site was subtracted and equated to the ecotone length of polygons. For structures defined by trees and bushes, the circumference calculated by ArcGIS Pro, was used and distance values were subtracted if the polygons edged the outline perimeter of the 150 m radius. Through this method, the ecotone length of trees and bushes was obtained. In summary, for each site, information on the number of polygons, ecotone length of all parts, ecotone length of trees and bushes, ecotone length of fields and the area of trees and bushes were filtered out.

2.6 Statistical analysis

All analyses were performed with the summed abundances of all collected bees during the sampling periods (1-8). Pan traps records were separated into two levels:

i) Sum of all records in all pan traps of a particular site (n = 7 if only considering RS-EF / PS-IF sites; n = 14 if considering all sites)

ii) Sum of the records in all pan traps of a specific colour, that is, white vs. yellow vs. blue of a particular site (n = 21 if only considering RS-EF / PS-IF sites; n = 42 if considering all sites)

First, a rarefaction curve was calculated with the online tool iNEXT (Chao et al. 2016) to see whether the sampling effort was sufficient to yield a representative dataset.

2.6.1 Distributions of wild bees

To illustrate differences in distributions of wild bees, honeybees, species richness, abundance and biomass, distribution charts were plotted and two-sample t-tests calculated. Moreover, the Shannon-Index and Evenness were applied to be able to distinguish variance of diversity on the sites.

Furthermore, two rank-abundance-dominance (RAD) curves were plotted. These graphs allowed us to identify the most abundant species and their associated functional traits. In a next step, the abundance was categorised following (Schwerdtfeger 1978) and species classified into eudominant (> 10%) and dominant ($\leq$ 10%). Diversity indices and RAD curves were carried out using Rstudio software 4.0.3 (RStudio Team 2020) and applying the "RADanalysis" and "vegan" packages (Saeedghalati et al. 2016; Oksanen et al. 2015).

To estimate whether assemblages differed in and among the sites and groups of sites, ANOSIM tests in PAST software 4.03 (Hammer 2001) were conducted. In total, four ANOSIM tests were computed using untransformed, square-root transformed, fourth-root transformed, and presence/absence data following Schlick-Steiner et al. (2006). The calculations settings used were Similarity Index Euclidean and 9999 random permutations. In a next step, a heatmap with abundance data was plotted to compare the outcoming results with the original dataset. Interpretation of R values followed the suggestions by Lin et al. (2003).

2.6.2 Regressions

Alongside the analysis of the bees' distributions, a main aim was to find out which environmental parameters explained the wild-bee communities best. To reduce the risk of autocorrelation, firstly particularly high correlations were checked for between the percentage of flower-colour abundance (percentage of white, yellow, blue flowers, drone flying height 10 m and percentage of white, yellow, blue flowers, drone flying height 20 m) and structural diversity (ecotone length of trees and bushes, ecotone length of fields, number of polygons, and areas of trees and bushes). To this end, three correlation matrices were designed: (1) involving data of all sites, (2) involving only extensively farmed sites (RS-EF) and (3) involving only sites with flowering strips (PS-IF). Strongly correlating variables with R > 0.75 and p < 0.05 were removed before further analysis. The results of correlation matrices revealed the variables ecotone length of trees and bushes, ecotone length of fields and number of polygons and drone height of 10 m above- ground to be best suitable (see Supplement 4-6).

In the following, simple linear regressions were conducted, using parameters of structure diversity or flower-colour abundance and wild bees' data. The accuracy of correlations was evaluated based on the coefficient of determination and significance testing. In addition, a canonical correlation analysis (CCA) was conducted to verify the results.

All regressions, correlation matrices and CCA were conducted using PAST (4.03).

3   Results

3.1   Bees' distributions

During the sampling period, we collected a total of 1988 wild bees, representing 117 species and 20 genera, as well as 2631 honeybees. Based on the results of DNA barcoding (Weigand unpublished 26-04-22), and morphological species identification, we did not identify species complexes to species level in two cases (*Andrena tibialis/bimaculata* referring to Schmidt et al. (2015); *Andrena cineraria/barbarae;* see Supplement 7).

The result of the rarefaction curve illustrates the sampling effort. Both curves flatten towards the end, but this trend is more visible for extensively farmed sites (RS-EF) than for fields with flowering strips (PS-IF) (see Figure 1). Most species belonged to the genus *Lasioglossum* (58.8% of all specimens) at 20 species, followed by *Andrena* (15.0%) at 27 species and *Bombus* (9.6%) counting 15 species (see Figure 2). About one third of total species number (36 species) were represented by just a single individual. Low abundances showed 76 species, making up 64.4% as they counted a maximum of five individuals. Wild bees' records were not distributed equally across sites as 1484 bees were caught on RS-EF but 504 individuals on PS-IF sites, featuring a significant difference in abundance ($p < 0.05$). RS-EF and PS-IF sites hosted 97 species equalling 56.1% of total biomass and 73 species equalling 43.9% of biomass, respectively. Average biomass per species was lower on RS-EF than on PS-IF sites (11.5 mg; 26.4 mg). Species richness and biomass between management types (RS-EF/PS-IF) differed significantly ($p = 0.01$ and $p = 0.012$, respectively).

The occurrence of the four selected species traits differed between management types: on RS-EF sites 6.9% of the bees belonged to (1) species specialised in pollen collection of a single plant species or genus (oligolectic). On PS-IF sites, oligolectic bees were more abundant (26.8%), as shown in Table 1. Considering (2) nesting strategies, on RS-EF sites, the below- ground nesting species were predominant (88.9%; 1320 specimens), compared with above- ground nesting bees, which made up 6.8% (101 specimens). Also on PS-IF sites, the proportion of above- ground nesting bees was lower at 6.0% (30 specimens) than that of below- ground nesting types (81.7%; 412 specimens). On RS-EF sites, (3) social bees were proportionally more abundant (62.9%) than solitary bees (30.3%), followed by parasitic bees (1.3%) and communally living bees (0.1%). On PS-IF sites, however, solitary bees represented the most abundant social type (55.8%) followed by social bees (34.5%), parasitic (4.8%) and communal bees (3.8%). The only communally living species detected was *Panurgus calcaratus,* which was collected mostly on PS-IF sites (19 of 21 specimen). Our data also showed differences in the distribution of (4) sex (here, *Bombus* queens and workers are combined). On RS-EF sites, male bees' proportion was represented by one of nine bees (10.3%) and one of four bees on PS-IF sites (20.6%).

3.2   Flower-colour abundance and distribution

Analysing drone pictures, we revealed differences in flower colours between management types. On the RS-EF sites, there were generally fewer flowers detected than on PS-IF sites (10 m drone flying height). Summing up the percentages of detected flower colours of the whole investigation period, the colour yellow was most abundant on PS-IF sites (6.1%). Yellow flowers also dominated on RS-EF sites making up 2.9% of the photographed area, followed by white flowers (1.1%) and blue flowers (0.6%). PS-IF sites showed a higher number of white flowers (4.0%) and a lower number of blue flowers (0.4%) than RS-EF sites. Summing up all flower colours, most colours (3.5%) could be detected at the end of Sampling Period 3 on the 26th of May. Thus, this was the day when most flowers were blooming.

3.3   Diversity of habitat structures

The average number of polygons on RS-EF sites (93.3) was higher than on PS-IF sites (57.4). RS-EF and PS-IF sites differed in the length of ecotones with 2311 m to 513 m and area of trees and bushes with 26,389 m² and 3843 m², respectively. An opposite trend showed the ecotone length of fields with lower values on RS-EF sites (3199 m) than on PS-IF sites (3726 m).

3.4   Bees' diversity of sites

Close to half of the species were collected on both groups of sites as they share in total 52 species. The community on sites with flowering strips host 70% of species also detected on RS-EF sites.

Comparing both groups, RS-EF sites featured a lower Shannon- Index than PS-IF sites, ranging from 1.62 to 2.79 and 2.60 to 3.21, respectively. Evenness ranged between 0.45 and 0.84 on RS-EF and between 0.79 and 0.90 on PS-IF sites. Since these observations were most pronounced at sites that hosted a high total number of bee individuals (EIG 3; TEL 7), low Evenness is explained by the occurrence of few highly abundant species. Sites with flowering strips (PS-IF) showed higher Shannon- Index values as a relatively large number of species were found despite lower abundances.

The rank- abundance analysis (RAD) confirmed this finding and adds more detail (see Figure 3 & 4). On RS-EF sites, we identified two species *Lasioglossum morio* (35.2%) and *Lasioglossum nigripes* (17.5%) to be eudominant (> 10%) but no species as dominant (≤10%). Both species represent endogaeic nesting and social types with relatively low average weight. The proportion of common species on PS-IF sites was distributed more even. Only *Lasioglossum calceatum* (14.1%) was detected to be eudominant and four species are categorised as dominant: *Eucera nigrescens* (8.3%), *Lasioglossum leucozonium* (6.5%), *Eucera longicornis* (5.6%) and *Andrena hattorfiana* (5.2%). *Eucera nigrescens*, *E. longicornis* and *Andrena hattorfiana* are oligolectic. All bee species mentioned here are below- ground nesting and apart of *Lasioglossum calceatum* solitary bees.

The results of ANOSIM testing showed further characteristics of beta diversity. Following the approach of Schlick-Steiner et al. (2006), we tested four levels of data accuracy to detect similarities and differences in species distribution. The lowest R value (R = 0.502; p = 0.001) was calculated with original abundance data, following presence/absence data (R = 0.599; p = 0.001) and interpreted as separated with a slight overlap. By computing with square root or fourth root, we relativised peaks in abundance data and levelled down the importance of the abundances of common species. This approach led to higher R values in square root transformation (R = 0.700; p = 0.001) and fourth root transformation (R = 0.825; p = 0.001).

A heatmap, showing bees' abundance data, helped to classify these results, and point out extreme values ("outlier") that may influence the data strongly (see Supplement 8). The heatmap illustrated that species that are not very common on RS-EF nor PS-IF sites were most relevant for shifts between RS-EF and PS-IF

sites. This finding applied to species like *Andrena vaga, Bombus bohemicus, Ceratina cyanea* and *Osmia aurulenta*. Exceptions from this assumption were for example *Bombus lucorum, Halictus tumulorum* and *Lasioglossum lativentre* – species common on both groups of sites. When considering eudominant and dominant species, there was an overlap in abundance on both sites. Differences were driven by highly abundant species like *Lasioglossum morio* and *Lasioglossum nigripes*, almost only collected on RS-EF sites and *Eucera nigripes* and *E. longicornis* mostly represented on PS-IF sites.

3.5   Impact of environmental parameters

The results of simple linear regressions revealed links between the selected parameters and wild bees' communities. We conducted regressions separately for two levels, that is i) sum of all records in all pan traps of a particular site; ii) sum of the records in all pan traps of a specific colour, that is, white vs. yellow vs. blue of a particular site (see 2.6).

The parameters ecotone length of trees and bushes, ecotone length of fields (excluding all woody elements, as defined in 2.5), number of polygons and blue flower colour all correlated positively with bees' variables, while yellow flowers were revealed to correlate partly negative. In more detail, wild bees' abundance correlated positively with ecotone length of trees and bushes ($R^2 = 0.33$; $p < 0.01$) as number of polygons ($R^2 = 0.19$; $p = 0.004$) and negatively with abundance of yellow flowers ($R^2 = 0.17$; $p = 0.006$), when considering ii) the sum of records in all blue, white, or yellow pan traps of all sites. The number of collected bees increased with blue flowers' abundance, when considering ii) on PS-IF sites only ($R^2 = 0.37$; $p = 0.003$).

Wild bees' biomass increased with the ecotone length of fields ($R^2 = 0.57$ $p < 0.05$), when considering level i) which includes the sum of all records in all pan traps of a particular site on RS-EF sites. However, neither ecotone length nor number of polygons were related significantly with bees' biomass. Also blue flower abundance impacted wild bees' biomass, in that this parameter correlated positively on both levels and sites: i) considering all records of all pan traps on PS-IF sites ($R^2 = 0.60$; $p < 0.05$); ii) considering the sum of records in all blue, white, or yellow pan traps of all sites ($R^2 = 0.10$; $p = 0.04$) and of PS-IF sites ($R^2 = 0.32$; $p = 0.007$).

The distribution of species richness can be explained by parameters of habitat structure as well as flowers colours, as it correlates slightly positively on level ii) considering all sites, with ecotone length of trees and bushes ($R^2 = 0.18$; $p = 0.005$) and blue flowers abundance ($R^2 = 0.14$; $p = 0.02$).

Although RS-EF sites dispose of a well-structured landscape and high number of ecotone length and small-scale diversity, we found no significant correlation between ecotone length of trees and bushes and any of the selected traits, when considering level i) on RS-EF sites. An exception represents the distribution of sex, as male bees decrease significantly with ecotone length ($R^2 = 0.56$; $p = 0.05$). When considering all sites, these structures do play a role as traits, dominant on RS-EF sites, increase significantly: Number of polylectic ($R^2 = 0.51$; $p = 0.003$); below- ground nesting ($R^2 = 0.38$; $p = 0.02$); above- ground nesting ($R^2 = 0.53$; $p < 0.003$); social ($R^2 = 0.55$; $p = 0.002$) and female ($R^2 = 0.46$; $p = 0.007$). Furthermore, oligolectic bees increased with ecotone length of fields ($R^2 = 0.31$; $p = 0.009$) and decrease with ecotone length of trees and bushes ($R^2 = 0.26$; $p = 0.02$), when considering ii) on RS-EF sites.

For PS-IF sites, the flower colours may contribute to the occurrence of specific species traits as numbers of oligolectic ($R^2 = 0.34$ $p = 0.005$), social ($R^2 = 0.18$; $p = 0.05$), solitary ($R^2 = 0.38$; $p = 0.003$) and parasite ($R^2 = 0.24$; $p = 0.04$) increased with the share of blue flowers on level ii).

Thus, our findings reflect the expectation on traits distribution due to environmental parameters. However, solitary bees were more abundant on PS-IF sites, than on RS-EF sites and show low dependency on diversity of habitat structures. Concerning foraging resources, we see a tendency towards more female bees on RS-EF sites and male bees on PS-IF sites.

These assumptions are supported by two CCAs, which illustrate the distribution of sites in their relation to the environmental parameters (see Supplement 9 & 10).

The sum of honeybees as well as the sum of wild bees were significantly higher on RS-EF sites than on PS-IF sites ($p = 0.027$ and $p = 0.001$, respectively). Honeybees' and wild bees' abundance showed a slightly positive ($R^2 = 0.10$), but non- significant correlation. Extremely high numbers of honeybees were collected on the three RS-EF sites ARZ1 (386), TEL6 (524) and TEL7 (370). These sites seem to be outliers, as honeybees' average abundance on remaining areas were lower (189 ± 136 specimens average) and on all remaining RS-EF sites honeybees were less abundant than wild bees. Most wild bees were collected on the RS-EF sites TEL7 (366), HAI5 (250) and EIG3 (242). On every PS-IF site, honeybees' number surpassed wild bees' abundance. Comparing honeybees' and wild bees' biomass, the biggest difference was detected on RS-EF sites (see Figure 5). When considering only single species, this difference is most extreme on TEL6 site, opposing one individual of *Andrena falsifica* (m) with 2.69 mg to 15385.41 mg biomass on honeybees and therefore representing a diminishing small fraction.

4   Discussion

Through this study, we aimed to compare wild bees' communities on extensively managed meadows in the Austrian Inn valley. The meadows are classified by the intensity of agricultural activities and the heterogeneity of habitat structures in the immediate environment. According to the two different management types, characterised by ether an extensively farmed, well-structured surrounding (RS-EF) or an intensively managed, low-structured environment (PS-IF), we distinguished functionally distinct wild bee communities. We collected 117 wild bee species, representing around 30% of species reported in Tyrol. RS-EF sites contain proportionally more polylectic, social, below- ground as above-ground nesting, female bees with a lower average of biomass as on PS-IF sites. In contrast, the wild-bee community on PS-IF sites was mainly determined by proportionally more oligolectic, solitary, parasitic and male bees with higher average biomass. Environmental structures proved to have an impact on the diversity and structure of wild bee communities. Especially the parameters ecotone length of trees and bushes and the flower colour blue correlated positively with the abundance of wild bees and their characteristics. Honeybees outnumbered the occurrence of wild bees at ten of 14 sites.

4.1   Sampling effort
The rarefaction curves show that the sampling effort was sufficient to collect most of the species of RS-EF sites, but we may still lack data on species on PS-IF sites. Additionally, it is important to mention that sampling through pan traps is known to collect some genera specifically over others (Cane et al. 2000; Toler et al. 2005). The success of the sampling method depends on floral abundance and species in the immediate environment (Westerberg et al. 2021; Toler et al. 2005; Baum and Wallen 2011). However, following the Proposal for an EU Pollinator Monitoring Scheme, pan-trap sampling is a standard method.

We could leverage the main advantage of this method in retrieving a large data set simultaneously without a researcher's bias (Westphal et al. 2008).

4.2   Community structure

In relation to the wild bees' total abundance on PS-IF sites, the species numbers and total biomass of bees on PS-IF sites were higher than expected. The alpha diversity on PS-IF sites was higher than on RS-EF sites, reflected by a higher average Shannon-index (2.84) and Evenness (0.87) values than on RS-EF sites (2.34 and 0.66, respectively). This leads to the conclusion that RS-EF sites are more valuable from a conservation point of view, as they host a broader and more site-specific range of species. Inferentially, wild bees' communities on PS-IF sites show more similarities among sites and seem to be more easily replaceable. However, we can derive, that PS-IF sites can offer suitable habitats for other bee species than those populating RS-EF sites, as 45 species only occurred on RS-EF sites and 21 species only on PS-IF sites. This assumption is supported by ANOSIM analysis, as we can examine both communities as well separated, when using fourth root transformation of data.

Based on the results of the RAD curves and the heatmap, we found that mainly dominant species define shifts in community structure. When looking at the species level, these common species, making up 5% to 10% of abundance data, may be the best indicators for environmental impacts, as they are often specialised on nesting or foraging resources (see Supplement 8). Eudominant species (> 10%) are mostly generalist species, not listed as threatened on the Red List of Germany or Switzerland for species at risk of extinction. *Lasioglossum nigripes* forms an exception, as it was collected in high numbers on RS-EF sites and especially on the particular site TEL7. This social bee species is known to nest on sand pits, dams, rough grassland, and ruderal sites (Westrich 2018) and is listed as strongly endangered (category 2) on the Red List of Germany (Westrich et al. 2011).

4.3   Impact of qualitatively and quantitatively high-grade resources within the wild bees' foraging distances

The results of our study indicate that bee communities depend on the investigated environmental parameters. As we see positive correlations between ecotone length and wild bee's abundance data, as well as number of polygons and wild bees' occurrence, we assume the probability for suitable nesting habitats and a diverse foraging supply to increase especially in highly structured landscapes. Fine- scale structures may also enhance the connectivity of habitats and thus have a positive impact on bees' abundance and diversity due to their reduced mobility. Flying distance is directly linked with flight duration and thus flying distance can be assumed to positively influence reproductive success (Zurbuchen et al. 2010a). Several studies show that with increasing foraging distance, nesting females can provide fewer brood cells. Moreover, brood cells are then filled with less pollen and nectar, and thus the survival rate for overwintering larvae is lower (Peterson and Roitberg 2006b; Seidelmann 2006). In addition, the probability of parasitism increases (Goodell 2003; Seidelmann 2006). Since bees' offspring is affected by increasing isolation of habitats (Williams and Kremen 2007), bees especially benefit from hedgerows, single trees, and forest edges that connect resources. To conclude from our data, bees' abundance and richness can be linked to a dense network of habitat patches. This finding is in line with the current state of research.

Concerning bees' biomass, we found significant correlation with just a single structural parameter (ecotone length of fields). PS-IF sites are low on small-scale structures defined by trees or bushes and provide more field margins, and thus isolation of habitats may increase. When taking a closer look at the collected species on PS-IF sites, the bees with highest biomass can be identified as bumblebees. On these sites, 14 of 15 species collected in this study were recorded with 94 individuals, which account for 18.7%

of total abundance. On RS-EF sites, *Bombus* species are represented by 14 species, too. These account only for 6.5% of total abundance. According to Steffan-Dewenter and Tscharntke (1999), isolated habitats are visited more often by larger bees, and bumblebees are less affected by increasing foraging distances. When comparing smaller species, we can identify higher abundances on RS-EF sites, as for example nine of ten *Hylaeus* species were collected on RS-EF sites and only three on PS-IF sites. Moreover, on RS-EF sites, we identified 19 *Lasioglossum* species with a total of 991 individuals (66.7%) and 14 *Lasioglossum* species with 177 individuals (35.1%) on PS-IF sites. These findings indicate structural diversity to be crucial not only for large but also for tiny species due to their low flying capacity and higher sensitivity to isolation (Gámez-Virués et al. 2015; Williams et al. 2010). Certainly, more detailed qualitative analyses of habitat structures might reveal further insights in the impact of heterogeneity of habitat structures on bee communities.

The quality of flowering margins enhances the foraging situation. On RS-EF sites, the abundance of flowers was less than on PS-IF sites, but the distribution of flower colours was more balanced. Especially the rising number of blue flower colours, caused by plant species known as relevant nectar and pollen resource (*Echium*, *Campanula*, *Vicia*; see Supplement 11) (Westrich 2018), seem to play an important role, as we found various correlations to wild bees' occurrence. Several studies confirm that not only quantitative, but the qualitative flower range can serve as a suitable proxy for bees' abundance (Roulston and Goodell 2011), as bee species richness is known to improve with increasing flowering plant diversity (Knop et al. 2006; Vulliamy et al. 2006).

Through our analysis, we revealed that yellow flower abundance correlates negatively with wild bee's abundance when considering all sites of RS-EF and PS-IF, but there was no significance when the two groups of sites were considered separately. We expect the difference in abundance data between the sites to have an impact on these findings. On PS-IF sites, yellow flowers dominated in the surrounding of the pan traps. On PS-IF sites, beside others, yellow blooms were often represented by common grassland genera like *Taraxacum, Ranunculus* and *Potentilla,* which provide important food resources (Westrich 2018) but are also known to indicate nutrient-rich meadows that only host a few flowering plant species (see Supplement 12) (Bohner 2010). As the total flower abundance is higher than on RS-EF sites, the quality of food resources or the lack of suiting nesting areas in the immediate surrounding might be limiting the population diversity. These findings can be related to another study that found the loss of nesting habitats to be the major driver of reduced bee abundance (Steffan-Dewenter and Schiele 2008). Moreover, only large bee species with high activity ranges may be able to visit large flower blooms and flowering strips, which remain until August. In the summertime, these structures may attract bees when the surrounding meadows are already mowed. Hence, we suggest PS-IF sites can serve as foraging habitats and foster bee species adapted to open areas. However, one needs to mention that our analysis only focused on the immediate environment and therefore did not take into account flower resources outside of the documented area (area size: 385 m²).

All the aforementioned findings lead us to the conclusion that well-structured sites can serve as nesting and foraging habitats and simplified landscapes with high flower abundance are mainly visited for nectar and pollen collection. Following recent literature, quality and quantity of habitat resources as well as connectivity between foraging and nesting structures are crucial to stabilize and enhance bees' communities (Zurbuchen and Müller 2012).

4.4 Species- specific adaptation to certain environmental parameters

Due to the different management types and structural compositions, we suggested links between specific habitats characteristics and species traits as well as differences in the distributions of traits between RS-EF and PS-IF sites.

On RS-EF sites, oligolectic pollen-collection behaviour increased with ecotone length of fields but decreased with ecotone length of trees and bushes. No significant correlations were revealed when considering all sites or only PS-IF sites. As the abundance of pollen-specialised bees are supposed to decline with decreasing diversity of land cover types and increasing average of patch size (Gámez-Virués et al. 2015), our results can only partly reflect these findings. Thus, not only structural diversity but foraging possibilities may act as a filter of functional- trait distribution. On PS-IF sites, in total more flowers were detected in the immediate surrounding of the pan traps and oligolectic bees especially correlated with blue flower colours. We suggest high values of bees with specialised feeding habits on PS-IF sites to be mainly driven by the dominantly occurring species *Andrena hattorfiana, Eucera nigrescens*, and *E. longicornis*. These species collect pollen preferentially on blue or purple flowers (e.g., *Knautia arvensis, Scabiosa columbaria; Vicia cracca, Lathyrus vernus*) (Westrich 2018) and can be classified as larger bees (female biomass 24.47 mg; 41.84 mg and 41.86 mg, respectively). These trends indicate that in our study, the occurrence of oligolectic bees on PS-IF sites may be mainly driven by specific flowering plant abundance in combination with structural compositions, as predominantly large oligolectic bees were collected.

Nesting behaviour was suggested to be mainly driven by land management intensity (Da Coutinho et al. 2018). As highly managed landscapes are expected to offer more open ground situations and thus possibilities for below- ground nesters (Klein et al. 2002), we assumed below- ground nesting bees to be less common in small-scaled habitats. However, we found both nesting types to be represented similarly on both management types. When considering all sites, below- ground nesting behaviour significantly correlated with ecotone length of trees and bushes and thus a heterogeneously structured landscape. The overall smaller sample size on PS-IF sites may have impeded retrieving a significant effect even though it does exist, as no significant correlations were found on PS-IF sites, when groups of sites are considered separately. Low abundance on PS-IF sites may be due to intensive soil cultivation and tillage, which can significantly impair below- ground nesting populations (Williams et al. 2010; Kim et al. 2006). However, above- ground nesting species are related positively to diversity of habitat structure and are more abundant on RS-EF sites. As they mostly nest in herbaceous or shrub stems, dead wood or snail shells (Westrich 2018), the intensification on cultivation and thus removing of such structures, affects epigaeic nesters negatively. Furthermore, above-ground nesting is found to be less common by increasing loss of connectivity between habitats (Williams et al. 2010).

Just as with the other bee traits, the distribution of social behaviour can also be linked to environmental parameters. Social bees were found to be more abundant on RS-EF sites and correlated positively with the abundance of ecotones, whereas abundance of solitary bees did not respond significantly to habitat structures. Both nesting types are supposed to decrease with increasing isolation, whereby social species are less sensitive to management intensification than solitary bees (Williams et al. 2010; Gathmann and Tscharntke 2002). Communal and parasitic bees were represented by only few species with low abundances. Both types of social behaviour were represented proportionally higher on PS-IF sites and parasitic bees were related positively to blue flower abundance. Thus, PS-IF sites are assumed to offer pollen resources for host bees and attract parasitic bees for nectar foraging.

Our results indicate a trend towards proportionally more female bees on RS-EF and a higher share of male bees on PS-IF sites. This distribution underlines our assumption of PS-IF sites lacking nesting resources and thus serving predominantly as foraging habitat. As male bees only forage for nectar, PS-IF sites may provide primarily nectar resources. Females' abundance, however, increased with ecotone length of trees and bushes (more abundant on RS-EF), indicating that these structures may improve the foraging and nesting situation.

Certainly, the dependencies between functional and ecological traits and environmental parameters are complex and specific responses are hard to distinguish. However, in most cases, our results are in line with the recent literature. It remains crucial to enhance high-quality, small-scale landscapes as the loss of these is directly correlated with a strong selection of species-trait compositions towards ubiquistic bees (Gámez-Virués et al. 2015). Moreover, several studies indicated the diversity in species guilds at a site to enhance pollination performance (Fründ et al. 2013; Hoehn et al. 2008; Klein et al. 2008).

4.5   Competition on foraging resources through honeybees

On particular RS-EF sites, honeybees (ARZ1; TEL6 and TEL7) and wild bees (TEL7; HAI5; EIG3) showed high abundances. On ARZ1 and TEL6, wild bees' abundance was less than would have been expected based on the high structural diversity and flower abundance. A possible explanation for the results for ARZ1 and TEL6 may be a high density of honeybee hives in the immediate surrounding. Interspecific competition on foraging resources between managed and native bee species is discussed controversially. Thomson (2006) detected that the abundance of bumblebees increased as the proximity to honeybee hives decreased. However, other studies did not reveal a significant response of bee diversity (Steffan-Dewenter and Tscharntke 2000). Honeybee colonies collect a considerable amount of pollen and nectar for larvae feeding and own flying supply. Keller et al. (2005) stated that in central European countries, the average amount of pollen, collected by one honeybee colony varies between 17 to 34 kg per year. As 426,121 hives were recorded in Austria in 2019 (Boigenzahn et al. 2021), we assume a reduced pollen availability for other foraging insects, where honeybee abundance is dense. Due to species-specific characteristics and beekeepers' management, honeybees' foraging activity is very efficient and advantageous over that of solitary bees: (1) Higher flying range of up to 10 km (Beekman and Ratnieks 2000); (2) endurance of bad weather conditions due to honey stock and feeding through beekeepers (Goulson 2003); (3) highly polylectic foraging strategy (Vorwohl 1972); (4) fast localisation and communication of foraging sites through bee dance (Esch et al. 2001); and (5) management by beekeepers by relocating hives near flowering blooms and treatment to avoid pests.

Observations indicate that wild bees evade to alternative pollen resources when honeybees' abundance increases (Walther-Hellwig et al. 2006; Shavit et al. 2009). Likewise, longer foraging distances and suboptimal quality of pollen affect the total reproduction and reduce fitness of wild bees' offspring (Paini and Roberts 2005; Goulson and Sparrow 2009). However, the results of our study do not reveal significant correlations of honeybee with wild bees' abundance.

4.6 Conclusion and management proposals

As Brown and Paxton (2009) reviewed, beside habitat loss and fragmentation, wild bees are exposed to a number of other threats, including invasive species (Stout and Morales 2009) and climate change (McCabe et al. 2022). These drivers of decline in species abundance are not independent factors and interact with each other (Brook et al. 2008). The loss of wild bee species can lead to a decrease of plant diversity (Biesmeijer et al. 2006) as flower- pollinator interactions are interfered. Likewise, mass-flowering cultivation affects not only wild bee communities, as they can enhance abundances of more generalistic foraging bees, but also leads to a decline of wildflowers abundance (Holzschuh et al. 2011). Thus, to ensure stable populations and their ecosystem services, it remains crucial to include conservation policy for pollinators in landscape use (Byrne and FitzPatrick 2009), including a beneficial habitat matrix of foraging and nesting resources. Further structures like the wildflower strips on PS-IF sites can not only enhance local species richness but also positively affect the surrounding areas (Marshall et al 2006). However, PS-IF sites cannot substitute well-structured habitats like on RS-EF sites, but wildflower strips can contribute to a more structured landscape. Thus, farmers can create food resources for wild bees with little effort by consciously managing marginal strips.

In poor-flowering areas, competition on foraging resources is likely (Thomson 2016). We expect competition to occur especially on RS-EF sites, as the abundance of honeybees is highest there. Thus, these species-rich sites should be preserved, and honeybee hives should not be set up within a radius of one to two kilometres from such sites (Zurbuchen and Müller 2012; Geldmann and González-Varo 2018). Moreover, knowledge on honeybee- wild bee interactions and their impact on further ecological networks should be generated. Finally, beekeeping should be distinguished from nature conservation practices as honeybees are used as agricultural animals (Geldmann and González-Varo 2018).

5 Author contributions

Beside Florian M. Steiner (Assoc.- Prof. Dr.) and Birgit C. Schlick-Steiner (Univ. - Prof. Dr. Mag.), Timo Kopf (Mag.) and Alexander M. Weigand (Dr.) contributed critically to the research project and shared their expertise.

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8 Figures and Tables

8.1 Figures

Figure 1 Rarefaction curves plotting bee species' richness against the number of collected individuals to interpretate samplings success. Curves for RS-EF and PS-IF flatten towards the end. Calculated with the online tool iNEXT (Chao et al. 2016).

RS-EF sites (rich structure, extensively farmed) and PS- IF sites (poorly structured, intensively farmed).
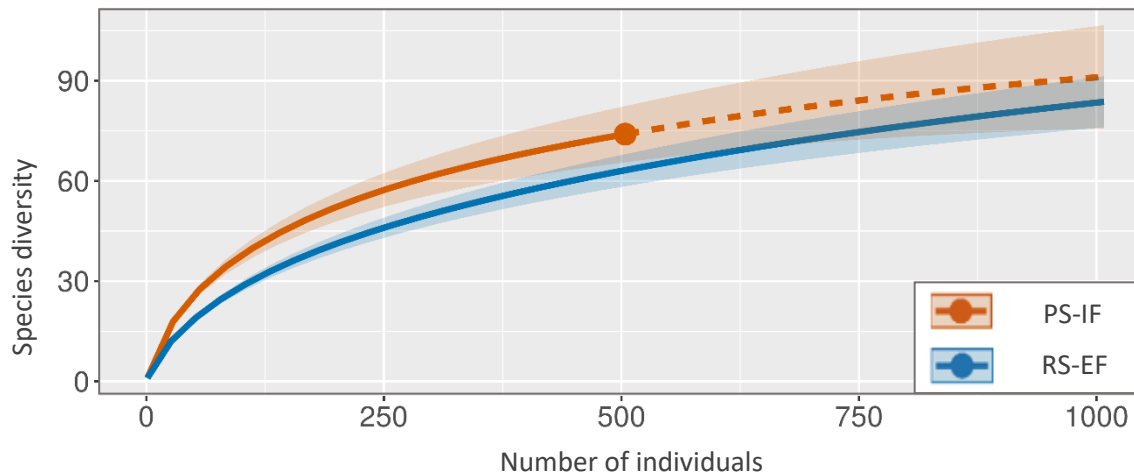
Figure 2 Pie chart on wild bee genus collected on the sampling sites, showing the most abundant species.
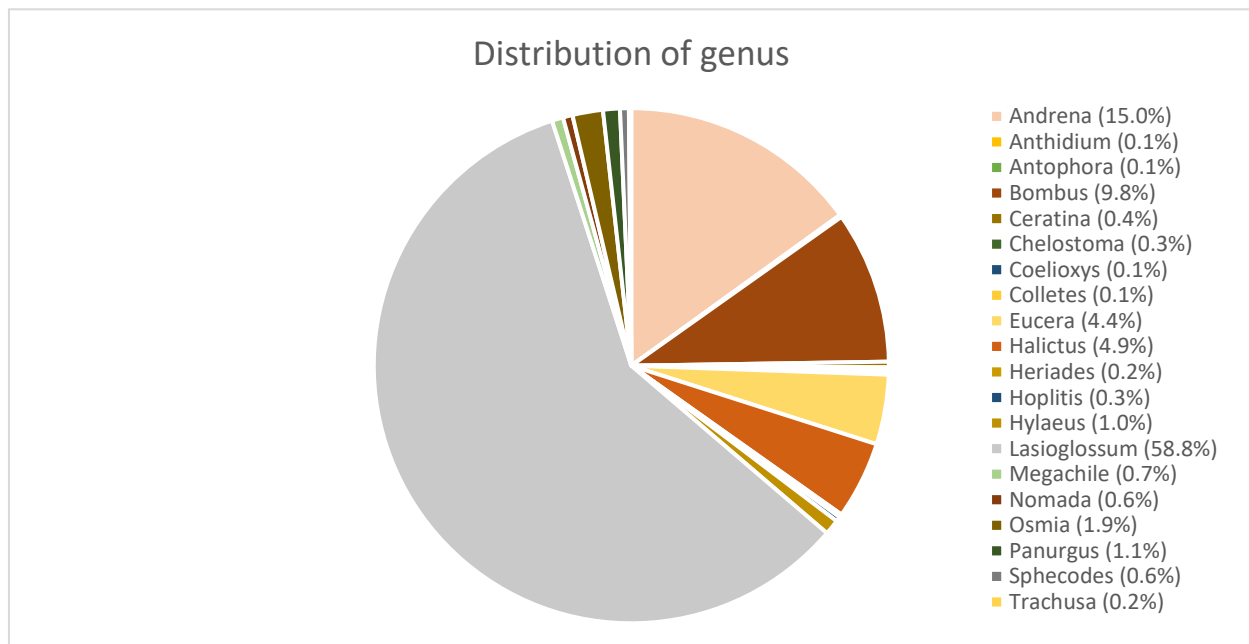
Figure 3 Rank- Abundance- Distribution (RS-EF sites) plotting the abundance of untransformed species data against rank order. Created in RStudio.
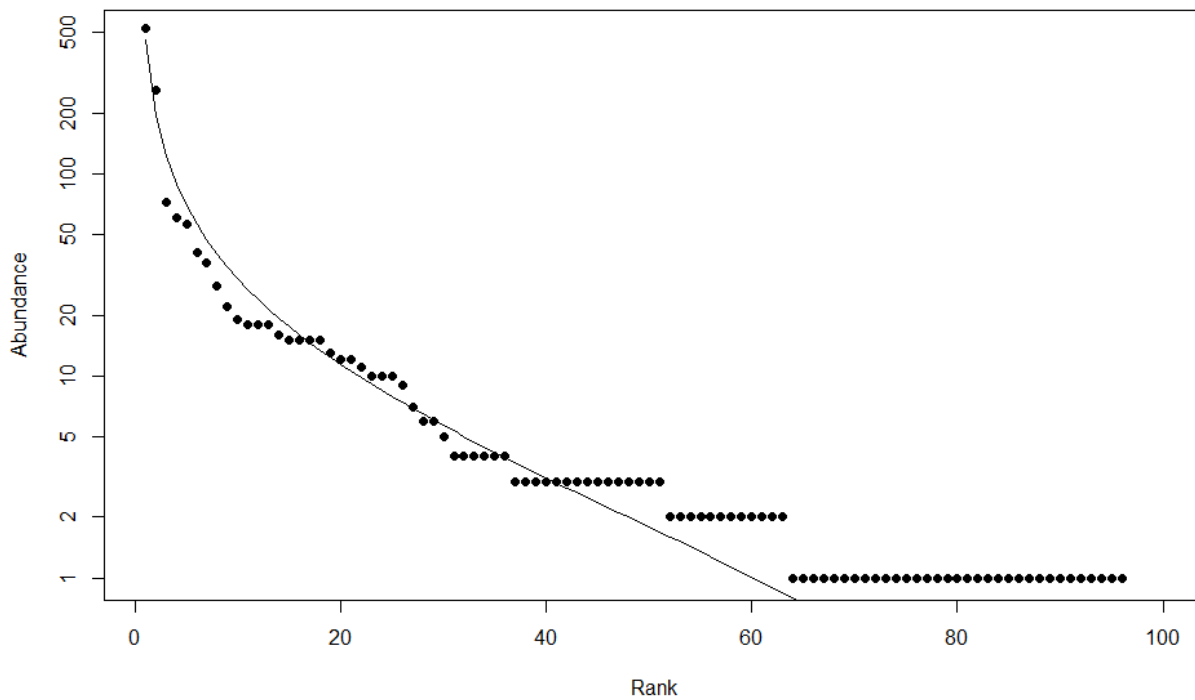
Figure 4 Rank- Abundance- Distribution (PS-IF sites) plotting the abundance of untransformed species data against rank order. Created in RStudio.
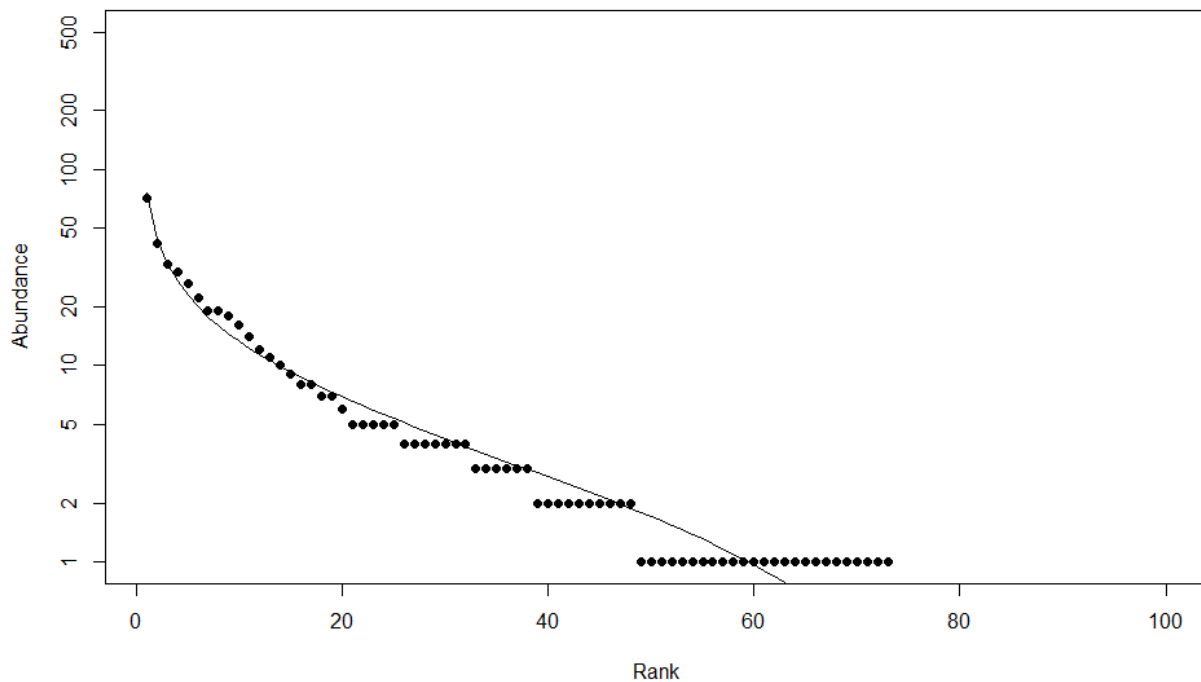
Figure 5 Boxplot diagram of wild bees' vs. honeybees' biomass on RS-EF (rich structure, extensively farmed) and PS-IF (poorly structured, intensively farmed) sites.

wb = wild bee; hb = honeybee; * = p < 0.05; ** = p < 0.01
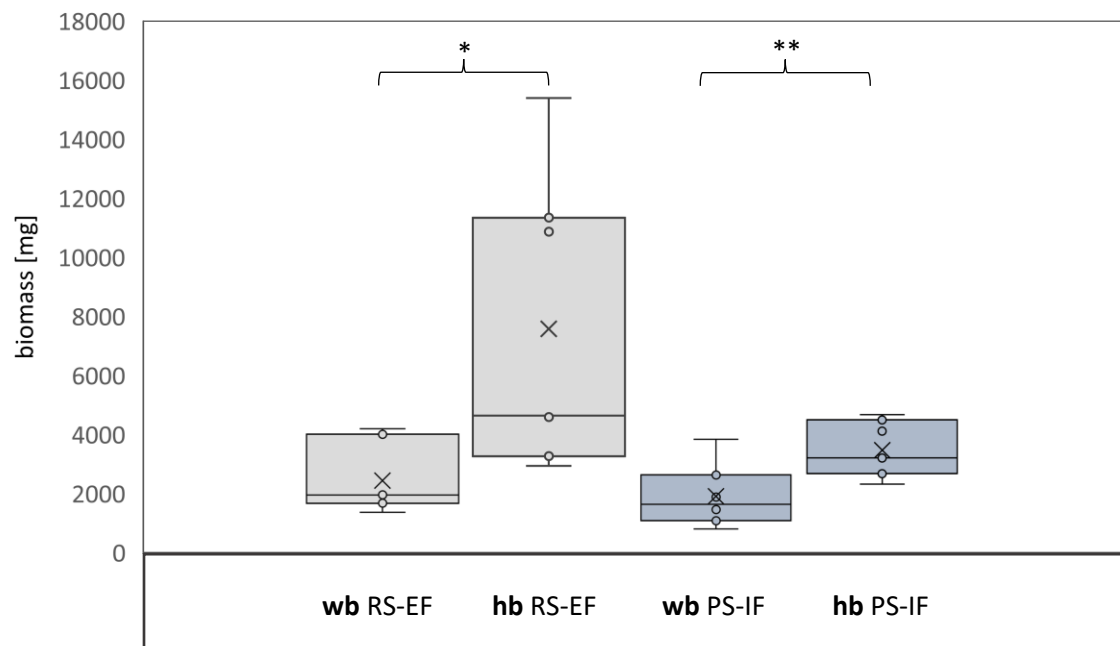
8.2 Tables

Table 1 Distribution of wild bees' ecological and functional traits on RS-EF sites (rich structure, extensively farmed surrounding) and PS-IF sites (poorly structured, intensively farmed surrounding).

	SITE	POLLEN COLLECTION			NESTING BEHAVIOUR					SOCIAL TYPE				SEX	
		OL	POL	NO	EN	EPI	NO	BO	SOC	SOL	PA	CO	UNK	F	M
RS-EF	ARZ1	8	88	1	78	15	1	3	59	37	1	0	0	86	11
	EIG2	10	156	2	140	21	2	5	97	63	2	1	5	143	25
	EIG3	3	237	2	212	21	2	7	175	61	2	0	4	223	19
	BRA4	5	198	6	179	16	6	8	99	75	6	0	29	164	45
	HAI5	53	193	4	235	4	4	7	104	114	4	0	28	214	36
	TEL6	11	138	3	127	12	3	10	96	46	3	1	6	144	8
	TEL7	12	352	2	349	12	2	3	303	53	2	0	8	357	9
PS-IF	BLU8	9	62	0	64	2	0	5	17	43	0	7	4	64	7
	BLU9	6	30	2	28	3	2	5	17	16	2	3	0	33	5
	BLU10	8	43	1	41	3	1	7	21	30	1	0	0	45	7
	BLU11	29	35	1	56	4	1	4	15	47	1	2	0	42	23
	BLU12	48	78	9	114	4	9	8	48	77	9	1	0	94	41
	BLU13	9	38	1	42	4	1	1	24	23	1	0	0	44	4
	BLU14	26	59	10	67	10	10	8	32	45	10	6	2	78	17
	SUM RS-EF	102	1362	20	1320	101	20	43	933	449	20	2	80	1331	153
	SUM PS-IF	135	345	24	412	30	24	38	174	281	24	19	6	400	104
	TOTAL	237	1707	44	1732	131	44	81	1107	730	44	21	90	1731	257
	RS-EF %	6.9	91.8	1.3	88.9	6.8	1.3	2.9	62.9	30.3	1.3	0.1	5.7	89.7	10.3
	PS-IF %	26.8	68.5	4.8	81.7	6.0	4.8	7.5	34.5	55.8	4.8	3.8	1.2	79.4	20.6

OL= oligolectic; POL= polylectic; NO = no collection/ nesting; EN = endogaic; EPI = epigaeic; BO = both; SOC = social; SOL = solitary; PA = parasite; CO = communal; UNK = unknown; F = female; M = male.

8.3   Supplements

Supplement 1 Study area between the cities of Innsbruck and Imst at the Inn valley (Tyrol), Austria. Sites 1-7 are well structured, extensively farmed sites (RS-EF); sites 8-14 are poorly structured, intensively farmed sites (PS-IF). Edited in ArcGis Pro; source of orthophotos: Land Tirol- data.gv.at.

Supplement 2 Reference pictures for RS-EF and PS-IF sites. Source: Pauline Bühler 2021.

RS-EF; EIG3   Pauline Bühler, 2021

RS-EF: ARZ1   Pauline Bühler, 2021

PS-IF; BLU 13   Pauline Bühler, 2021

Supplement 3 Python script (Source: Marlene Haider) applied in Anaconda Navigator 2.1.1 (Anon 2020) to evaluate drone images.

```python
In [1]: import cv2

        ## Read
        img = cv2.imread("Picture.tiff")
        ## convert to hsv
        hsv = cv2.cvtColor(img, cv2.COLOR_BGR2HSV)

        ## mask of white
        whiteSensitivity = 40
        maskW = cv2.inRange(hsv, (0, 0, 255-whiteSensitivity), (255, whiteSensitivity, 255))

        ## mask of yellow
        yellowSensitivity = 80
        maskY = cv2.inRange(hsv, (20, yellowSensitivity, 255-yellowSensitivity), (45, 255, 255))

        ## mask of blue (picture, (LowerRange), (upperRange))
        maskB = cv2.inRange(hsv, (80,64, 0), (155, 255, 255))

        #choose mask for target
        mask = maskY

        # print mask on target
        target = cv2.bitwise_and(img, img, mask=mask)

        #save new image with mask
        cv2.imwrite("PictureB.jpg", target)

        #percent of mask
        percentage = (mask>0).mean()*100
        print(percentage)
```

Supplement 4 Correlation matrices, showing the correlation coefficients between the variables. Highly correlating (R <0.75) and significant (p<0.05) variables are sorted out to avoid autocorrelation in further analysis. This table shows the correlation matrix including ALL sites. Computed with PAST software 4.03 (Hammer 2001).

	tree_area	oeco_length	oeco_tree	oeco_fields	nbr_parts	white_10	yellow_10	blue_10	white_20	yellow_20	blue_20
tree_area		0.5177	0.1035	0.0001	0.9828	0.1554	0.1349	0.6941	0.8335	0.0461	0.0143
oeco_length	-0.1027		0.2551	0.4779	0.0000	0.0099	0.0014	0.7690	0.0171	0.0007	0.5443
oeco_tree	0.6234	0.6012		0.0563	0.0159	0.0360	0.0633	0.5595	0.2679	0.0185	0.2480
oeco_fields	-0.7555	0.5847	-0.2968		0.0040	0.3724	0.0766	0.8099	0.0963	0.1383	0.0535
nbr_parts	0.0034	0.9289	0.6645	0.4354		0.0366	0.0017	0.2830	0.0757	0.0023	0.0842
white_10	-0.2232	-0.3938	-0.3245	-0.1412	-0.3235		0.0201	0.7815	0.0000	0.1359	0.6408
yellow_10	-0.2346	-0.4767	-0.2891	-0.2762	-0.4700	0.6598		0.5221	0.0001	0.0000	0.3689
blue_10	0.0625	-0.0467	-0.0927	0.0383	-0.1696	-0.0441	0.1016		0.8266	0.9964	0.0000
white_20	-0.0334	-0.3662	-0.1749	-0.2600	-0.2770	0.9489	0.5596	-0.0348		0.0010	0.9883
yellow_20	-0.3094	-0.5021	-0.3620	-0.2326	-0.4582	0.6169	0.9424	-0.0007	0.4904		0.8999
blue_20	0.3754	-0.0962	0.1823	-0.3000	-0.2697	-0.0741	0.1422	0.7624	-0.0023	-0.0200	

Supplement 5 Correlation matrices showing the correlation coefficients for RS-EF sites. Computed with PAST software 4.03 (Hammer 2001).

	tree_area	oeco_length	oeco_tree	oeco_fields	nbr_parts	white_10	yellow_10	blue_10	white_20	yellow_20	blue_20
tree_area		0.1294	0.5649	0.0000	0.0003	0.6854	0.3552	0.4608	0.2431	0.4667	0.3516
oeco_length	-0.8008		0.0563	0.0319	0.0000	0.7635	0.3887	0.3432	0.4202	0.6733	0.0688
oeco_tree	0.1332	0.4227		0.2963	0.0614	0.2270	0.2477	0.0050	0.1425	0.1443	0.3803
oeco_fields	-0.9502	0.7788	-0.2392		0.0003	0.2449	0.0762	0.4502	0.0528	0.1402	0.1960
nbr_parts	-0.7076	0.9335	0.4150	0.7129		0.7669	0.0769	0.0549	0.3356	0.3788	0.0005
white_10	0.0939	-0.0698	0.2754	-0.2654	-0.0688		0.3259	0.3331	0.0000	0.4126	0.2202
yellow_10	0.2125	-0.1984	0.2639	-0.3952	-0.3944	0.2254		0.1244	0.1030	0.0000	0.0013
blue_10	-0.1702	-0.2177	-0.5886	0.1742	-0.4248	0.2221	0.3460		0.2661	0.3729	0.6506
white_20	0.2664	-0.1858	0.3312	-0.4282	-0.2211	0.9710	0.3658	0.2543		0.1934	0.0564
yellow_20	0.1680	-0.0978	0.3298	-0.3330	-0.2025	0.1887	0.9374	0.2049	0.2955		0.0845
blue_20	0.2140	-0.4047	-0.2018	-0.2939	-0.6906	0.2793	0.6528	0.7595	0.4224	0.3853	

Supplement 6 Correlation matrices showing the correlation coefficients for RS-EF sites. Computed with PAST software 4.03 (Hammer 2001).

	tree_area	oeco_length	oeco_tree	oeco_fields	nbr_parts	white_10	yellow_10	blue_10	white_20	yellow_20	blue_20
tree_area		0.4662	0.0046	0.0318	0.6685	0.0008	0.2021	0.8725	0.0000	0.5495	0.0558
oeco_length	-0.1682		0.0597	0.0003	0.0107	0.2688	0.0440	0.5307	0.1896	0.0053	0.2103
oeco_tree	0.5927	0.4175		0.9302	0.0003	0.0159	0.1323	0.8248	0.0208	0.8204	0.0007
oeco_fields	-0.4693	0.9000	-0.0204		0.0047	0.0141	0.0014	0.4243	0.0072	0.0009	0.9539
nbr_parts	0.0993	0.8500	0.7147	0.5924		0.9226	0.4619	0.5850	0.8822	0.2044	0.0302
white_10	0.8873	-0.2529	0.5190	-0.5271	0.0226		0.0033	0.5126	0.0000	0.0185	0.1648
yellow_10	0.2901	-0.4435	0.3394	-0.6508	-0.1698	0.6109		0.1008	0.0272	0.0001	0.4007
blue_10	0.0373	-0.1450	0.0514	-0.1841	-0.1264	0.1513	0.3679		0.8873	0.2580	0.0006
white_20	0.9568	-0.2980	0.5007	-0.5680	-0.0344	0.9698	0.4813	0.0329		0.1003	0.2356
yellow_20	0.1385	-0.5853	0.0527	-0.6692	-0.2887	0.5090	0.9103	0.2584	0.3685		0.7810
blue_20	0.4234	0.2851	0.6821	-0.0134	0.4733	0.3146	0.1935	0.6865	0.2705	-0.0646	

tree_area = area of trees and hedges; oeco_length = ecotone length of all polygons; oeco_tree = ecotone length of trees and hedges; eco_fields = ecotone length of all polygons but trees and hedges; nbr_parts = number of polygons; white_10 = abundance of white flowers, drone flight hight 10 m; yellow_10 = abundance of yellow flowers, drone flight hight 10 m; blue_10 = abundance of blue flowers, drone flight hight 10 m; white_20 = abundance of white flowers, drone flight hight 20 m; yellow_20 = abundance of yellow flowers, drone flight hight 20 m; blue_20 = abundance of blue flowers, drone flight hight 20 m.

Supplement 7 Results of DNA- barcoding of wild bees collected on the study sites. National Museum of Natural History, Luxembourg ((Weigand unpublished 26-04-22).

morphological determination	DNA- barcoding	BOLD BIN
Andrena wilkella/ovatula	*Andrena wilkella*	BOLD:ABZ0235
Andrena tibialis/bimaculata	*Andrena bimaculata / A. tibialis*	BOLD:AAK0349
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena cineraria/ barbarae	*Andrena cineraria*	
Andrena ovatula/ovatula	*Andrena ovatula*	BOLD:AAP2754
Andrena wilkella/ovatula	*Andrena ovatula*	BOLD:AAP2754
Bombus hortorum/hortorum	*Bombus hortorum*	BOLD:AAD2566
Bombus ruderatus/hortorum	*Bombus hortorum*	BOLD:AAD2566
Andrena tibialis/bimaculata	no result	
Andrena ovatula/ovatula	no result	
Andrena pandellei	no result	
Lasioglossum interruptum	no result	
Osmia labialis	no result	

Supplement 8 Heatmap of wild bees' abundance on the study sites. Gradient of green colour refers to number of bees per species. Yellow marked species are classified as eudominant (> 10%) and dominant (≤ 10%).

A. = *Andrena*, An. = *Anthophora*; Ant. = *Anthidium*; B. = *Bombus*, Ch. = *Chelostoma*, C. = *Ceratina*, Co. = *Coelioxys*, Coll. = *Colletes*; E. = *Eucera*; H. = *Halictus*; He. = *Heriades*; Ho. = *Hoplitis*; Hy = *Hyleaus*; L. = *Lasioglossum*; M. = *Megachile*; N. = *Nomada*; O. = *Osmia*; P. = *Panurgus;* Sp. = *Specodes*; T. = *Trachusa.*

ARZ1; EIG2; EIG3; BRA4; HAI5; TEL6; TEL7 = sites with rich structure, extensively farmed (RS-EF).

BLU8; BLU9; BLU10; BLU11; BLU12; BLU13; BLU14 = sites poorly structured and intensively farmed surrounding (PS-IF).

site	ARZ1	EIG2	EIG3	BRA4	HAI5	TEL6	TEL7	BLU8	BLU9	BLU10	BLU11	BLU12	BLU13	BLU14	SUM RS-EF	SUM PS-IF
A. alfkenella	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
A. bicolor	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
A. carantonica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
A. cineraria/barbarae	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	3
A. dorsata	0	1	0	0	0	0	0	2	0	1	0	0	0	0	1	3
A. falsifica	0	0	0	0	2	1	0	0	0	0	0	0	0	0	3	0
A. flavipes	1	10	12	26	12	6	5	2	0	1	0	0	0	1	72	4
A. fulva	1	0	0	0	0	0	0	2	0	0	0	0	0	0	1	2
A. fulvida	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
A. gravida	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
A. haemorrhoa	0	0	0	0	1	0	0	4	6	0	5	2	1	4	1	22
A. hattorfiana	0	4	0	2	1	3	0	0	1	5	4	4	2	10	10	26
A. humilis	1	0	0	0	1	6	10	0	2	1	1	0	0	0	18	4
A. intermedia	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
A. labiata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
A. lathyri	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
A. minutuloides	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
A. nigroaeanea	0	2	2	3	7	2	2	0	0	1	1	3	3	1	18	9
A. nitida	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	4
A. ovatula	0	2	8	3	11	0	4	2	0	0	0	1	0	0	28	3
A. pandellei	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
A. praecox	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1

A. subopaca	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1
A. tibialis/bimaculata	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1
A. vaga	5	0	0	0	35	1	0	0	0	0	0	0	0	5	41	5
A. ventralis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
A. wilkella	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2	0
A. punctatum	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0
An. aestivalis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
B. argillaceus	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1
B. bohemicus	0	1	1	1	0	0	0	0	0	1	1	2	1	7	3	12
B. campestris	0	1	0	0	0	3	0	0	0	0	0	0	0	0	4	0
B. cryptarum	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	2
B. hortorum	0	2	0	0	1	3	0	3	0	1	1	1	1	1	6	8
B. humilis	1	1	4	1	2	3	3	0	0	1	0	1	1	2	15	5
B. jonellus	0	0	0	2	1	0	0	0	0	0	2	0	2	3	4
B. lapidarius	2	0	2	0	0	0	0	0	1	0	0	0	0	1	4	2
B. lucorum	1	1	2	2	8	1	3	1	0	1	3	5	5	4	18	19
B. pascuorum	0	2	5	1	1	2	1	0	3	4	3	3	0	3	12	16
B. pratorum	0	1	2	0	0	2	0	0	1	0	1	1	2	1	5	6
B. ruderarius	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	3
B. soroeensis	0	1	0	1	0	1	0	0	0	1	0	0	1	0	3	2
B. sylvarum	1	0	0	0	4	3	1	1	1	0	0	2	0	0	9	4
B. terrestris	1	0	0	0	9	2	0	1	4	0	0	3	0	2	12	10
C. cyanea	0	2	3	1	0	1	0	0	0	0	0	0	0	0	7	0
Ch. distinctum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Ch. florisomne	0	3	0	0	0	0	0	0	0	0	1	0	0	0	3	1
Co. conoideus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Co. mandibularis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Coll. cunicularius	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
E. longicornis	0	0	0	0	0	0	0	1	0	1	17	7	4	0	0	30
E. nigrescens	1	0	0	0	14	0	0	0	0	0	3	35	2	2	15	42
H. confusus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
H. maculatus	2	0	0	0	1	0	0	0	1	0	0	0	0	0	3	1

H. scabiosae	0	0	0	0	0	1	1	0	0	0	1	1	0	0	2	2
H. simplex	8	3	6	5	12	10	12	6	1	0	1	2	1	0	56	11
H. subauratus	0	0	1	1	0	2	0	0	0	0	0	0	0	0	4	0
H. tumulorum	4	0	0	1	0	3	2	1	0	1	0	1	0	4	10	7
He. truncorum	1	0	0	1	1	0	1	0	0	0	0	0	0	0	4	0
Ho. adunca	0	1	2	0	0	0	0	0	0	0	0	0	0	0	3	0
Ho. leucomelana	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0
Ho. mitis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Hy. angustatus	0	2	1	1	0	0	0	0	0	0	0	0	0	0	4	0
Hy. brevicornis	0	3	0	0	0	0	0	1	0	0	0	0	0	0	3	1
Hy. communis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Hy. confusus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Hy. gredleri	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Hy. hyalinatus	0	1	0	0	0	0	1	0	0	0	0	0	0	0	2	0
Hy. nigritus	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Hy. paulus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Hy. sinuatus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hy. styriacus	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1
L. aeratum	0	0	1	25	27	3	5	4	0	0	0	0	0	0	61	4
L. albipes	0	1	0	1	0	1	0	0	0	0	0	0	0	2	3	2
L. calceatum	5	0	1	1	4	2	2	8	7	10	5	24	11	6	15	71
L. convexiusculum	0	0	2	0	0	1	0	0	0	0	0	0	0	0	3	0
L. fulvicorne	1	15	8	9	1	0	2	0	0	0	0	1	0	0	36	1
L. interruptum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
L. laticeps	0	0	0	1	1	0	0	0	0	1	0	3	0	1	2	5
L. lativentre	1	2	4	6	6	2	1	9	1	0	1	2	4	1	22	18
L. leucopus	0	0	0	0	1	0	0	2	0	6	0	2	0	4	1	14
L. leucozonium	0	1	0	2	3	7	3	7	1	6	1	5	2	11	16	33
L. lucidulum	0	0	1	0	0	0	0	1	0	2	0	0	0	0	1	3
L. morio	22	82	157	83	61	56	61	1	0	0	1	0	0	2	522	4
L. nigripes	3	4	0	3	11	14	225	0	0	0	1	1	1	2	260	5
L. nitidulum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0

Species	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	Sum1	Sum2
L. pauxillum	10	0	0	0	0	0	1	0	0	0	0	0	0	0	11	0
L. politum	9	2	1	2	0	2	3	0	0	0	0	0	0	0	19	0
L. punctatissimum	0	4	1	3	1	1	3	0	0	0	0	0	0	0	13	0
L. sexnotatum	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2
L. villosulum	0	0	0	0	1	0	0	0	0	0	0	7	0	0	1	7
L. zonulum	1	0	0	0	0	1	1	1	1	2	2	1	0	1	3	8
M. centuncularis	0	1	0	0	0	0	1	0	0	0	0	0	0	1	2	1
M. circumcincta	0	0	0	4	0	0	0	0	0	0	0	0	0	0	4	0
M. ligniseca	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
M. versicolor	0	0	0	1	0	2	0	1	0	2	0	0	0	0	3	3
N. armata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
N. ferruginata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
N. fulvicornis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
N. lathburiana	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0
N. leucophthalma	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
N. sexfasciata	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
O. aurulenta	0	0	0	0	0	1	2	0	0	0	0	0	0	0	3	0
O. bicolor	1	0	3	4	0	1	1	0	0	0	0	0	0	0	10	0
O. bicornis	7	3	1	2	0	1	1	0	0	0	2	0	0	0	15	2
O. caerulescens	0	1	4	0	1	0	0	0	0	0	0	0	0	0	6	0
O. labialis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
O. xanthomelana	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
P. calcaratus	0	1	0	0	0	1	0	7	3	0	2	1	0	6	2	19
Sp. albilabris	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Sp. crassus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sp. ephippius	0	0	0	1	2	0	0	0	0	0	0	1	0	1	3	2
Sp. ferruginatus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Sp. geoffrellus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Sp. niger	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Sp. puncticeps	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
T. byssina	0	0	1	0	0	0	1	0	0	1	0	0	0	0	2	1

Supplement 9 Canonical Correspondence Analysis (CCA). Species distribution due to ecological parameters. Computed in PAST software 4.03 (Hammer 2001).
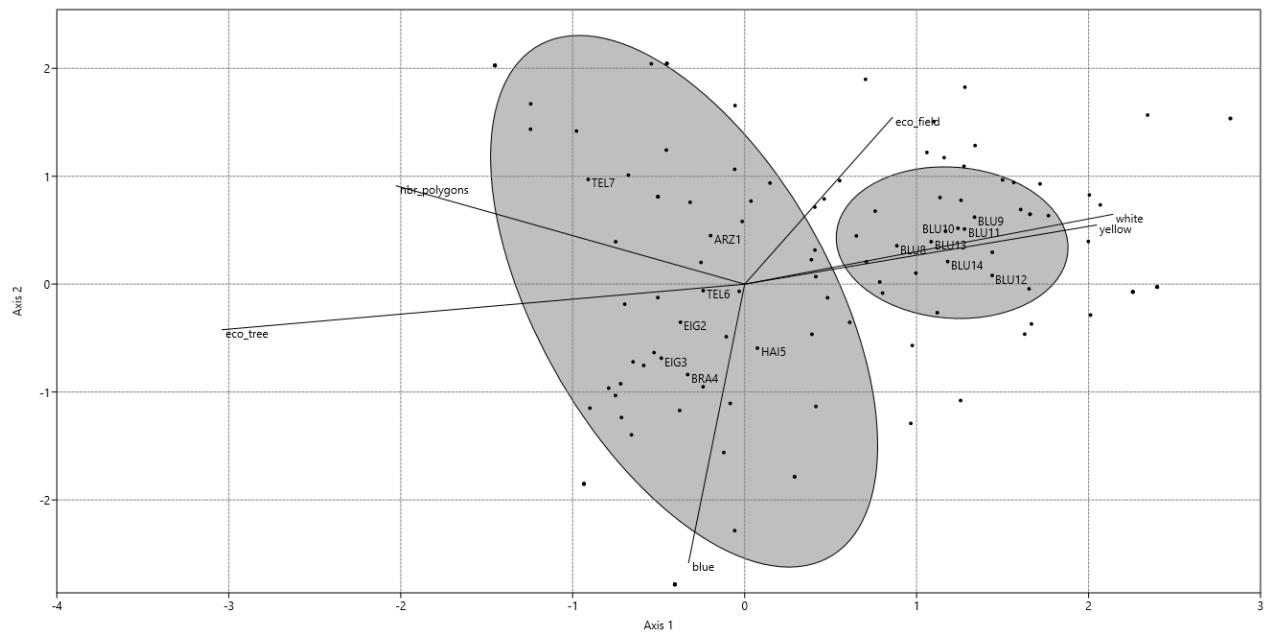
Supplement 10 Canonical Correspondence Analysis (CCA).) Distribution of functional and ecological traits due to ecological parameters. Computed in PAST software 4.03 (Hammer 2001).
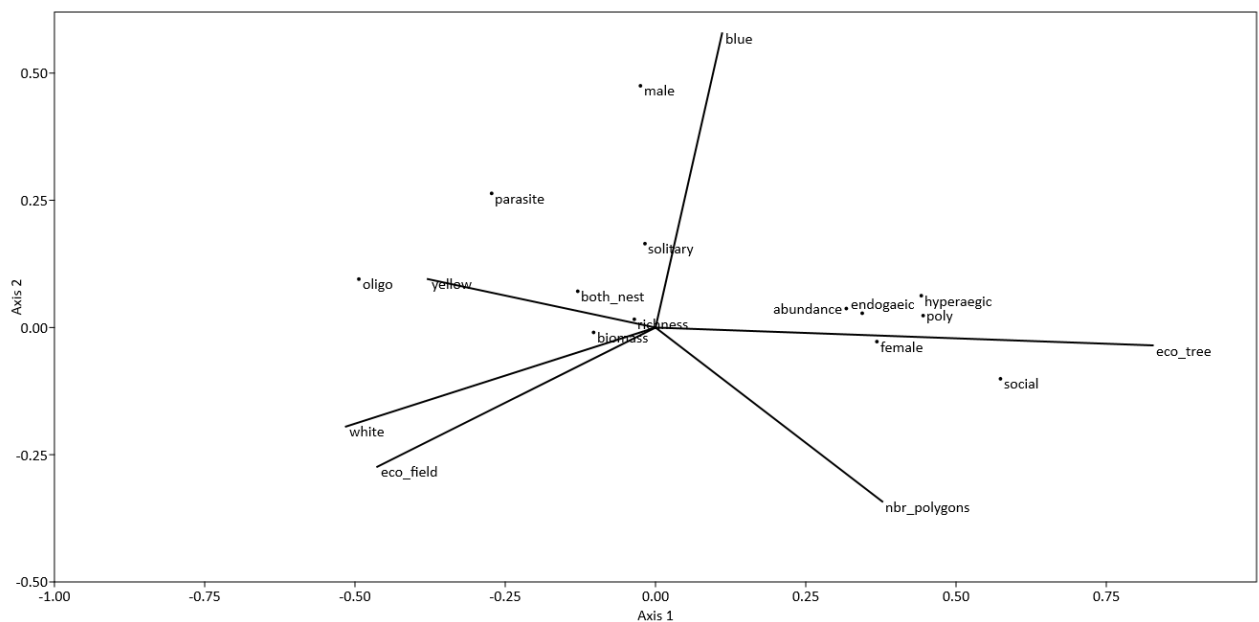
Supplement 11 Selection on blue or purple flowers on RS-EF sites (Source: Pauline Bühler, 2021)

Pauline Bühler, 2021

Pauline Bühler, 2021

Pauline Bühler, 2021

Supplement 12 Selection on yellow or white flowers on PS-IF sites (Source: Anna Biasi, Marvin Hopp,2021)

Marvin Hopp, 2021

Marvin Hopp, 2021

Anna Biasi, 2021

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt durch meine eigenhändige Unterschrift, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Alle Stellen, die wörtlich oder inhaltlich den angegebenen Quellen entnommen wurden, sind als solche kenntlich gemacht.

Die vorliegende Arbeit wurde bisher in gleicher oder ähnlicher Form noch nicht als Magister-/Master-/Diplomarbeit/Dissertation eingereicht.

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