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„Impact of inundation regime and meadow management on
wild bee communities and bee-flower networks in the
National Park Donau-Auen“

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Introduction

Wild bees are a functionally important component of grassland biodiversity in Central Europe. They provide vital pollination service for most flowering plants, yet also play a role as hosts to highly specialist parasites such as cuckoo bees (Zurbuchen & Müller, 2012; Nicholls & Altieri, 2013). Wild bees require a number of different resources such as species-specific nest sites, specific materials for nest construction, nectar sources to provide nourishment for adult bees and pollen as the essential component of larval food. Some oligolectic bee species depend on the pollen of individual plant families or even genera. Accordingly, only an environment with a manifold supply of different flowering plants and rich in structural complexity can fulfil the needs of a diverse bee community. Furthermore, this implies that sites which offer a different spectrum of pollen sources and structural elements will house differing bee communities (Westrich, 1996).

The persistence of plant and animal populations in agricultural landscapes is important for both, maintaining ecosystem services and the conservation of threatened species. On the one hand, insects such as wild bees suffer from land use intensification and ongoing landscape change and many species show negative population trends (Kremen et al., 2002; Öckinger & Smith, 2007; Scheper et al. 2014; Woodcock et al. 2016). On the other hand, after the destruction of natural habitats, man-made semi-natural habitats are some of the most species-rich remaining habitat types in central Europe. These habitat types have traditionally been maintained by extensive land use, such as grazing or mowing, and are dependent on continuous management to preserve their characteristic flora and fauna. Intensity of management by grazing or mowing is known to alter the species composition and structure of grassland vegetation, and intermediate levels of disturbance are assumed to increase plant species richness and to reduce the dominance of otherwise competitively superior species (Steffan-Dewenter & Leschke, 2003; Weiner et al., 2011; Wastian et al., 2016).

In areas close to running waters disturbance can be caused by flooding due to rising water levels (Gerisch et al., 2012). Fies et al. (2016) observed butterfly communities along an inundation gradient and found that butterfly abundance and species richness were lower on meadows with stronger flood impact. Furthermore Fellendorf et al. (2004) described a massive population decline of two aggregations of *Andrena vaga* which were situated in the floodplain area located in the upper Rhine valley after a flooding event in May 1999. *Andrena*

vaga is a non-social, soil-nesting bee and hence prone to mortality during inundation episodes. On the long term, flooding events alter the composition and diversity of plant communities (Sher et al., 2000; Wang & Zhu, 2001), which subsequently translates into changes of bee communities in affected areas (Westrich, 1996). Several studies suggest that regular flooding events result in distinct vegetation types, which can promote a higher beta diversity of the inhabiting fauna (Looy et al., 2003; Wittmann et al., 2006; Melo et al., 2009). Under the premise that bee communities show a sufficient resilience to flooding this could possibly even increase overall bee diversity on more often inundated meadows as compared to non-flooded meadows. Strong resilience to flooding was already described for ground beetles by Gerisch et al. (2012) and Truxa and Fiedler (2012) even found a slightly richer moth fauna in floodplain forests than in neighboring non-flooded forest habitats

However, certain species may suffer more strongly from flood-associated mortality than others, which could lead to persistent community shifts. Demetz et al. (2013) found no effect of regular flood events on species richness of grasshopper assemblages in the Donau-Auen national park but were able to detect a strong effect on the species composition of grasshopper assemblages, which was related to the regularity of flooding. Among wild bees for example, *Lasioglossum marginatum*, which has become one of the most common and dominant bee species in east Austria over the last years (Pachinger et al., 2014; Pachinger, 2002), could be exceptionally strongly influenced by recurrent inundations. This is the only Central European native wild bee species whose queens can reach up to 6 years of age. During the first 4 to 5 years the queen only produces female workers. Only afterwards, once the colony comprises 160 to over 1450 inhabitants, the single queen starts to produce fertile males and females. Consequently, it must be difficult for *Lasioglossum marginatum* to colonize highly dynamic areas which underlie regular disturbance events that result in complete local extinction. *Lasioglossum marginatum*, like *Andrena vaga*, is a soil nesting bee. It is only logical that inundation events with water covering the nesting sites for several days to weeks must have disastrous consequences on affected colonies (Fellendorf et al., 2004; Scheuchl & Willner, 2016).

While responses of bee assemblages to environmental gradients such as land use intensity and flooding regime have been documented in some cases (Fellendorf et al., 2004; Weiner et al., 2011), much less is known about the biotic networks that result from interactions between

flowers and bees. These two-sided relationships between flowers and bees create bipartite networks meaning that every member of one trophic level is connected to one or multiple representatives of the other trophic level (Jordano et al., 2003). With this analytical approach, direct interactions within trophic levels (e.g. competition, intra-guild predation) are ignored. Prominent recent examples of network analyses include pollination webs, species-rich predator-prey systems and seed dispersal mutualisms (Blüthgen et al., 2007; Dormann et al., 2008, Power et al., 2011). A bipartite network analysis can provide profound insights into the characteristics of a community and especially into the strength of dependencies between species (Dormann et al., 2008). Additionally, bipartite networks provide information that can help to identify crucial players in the network, commonly called keystone species (Bascompte et al., 2006). In recent years, such bipartite networks have matured into an important paradigm to study the diversity of interspecific interactions and ecosystem functions (Dormann et al., 2009).

Since 2008 the package “bipartite” in the statistical R environment (Dormann et al. 2016) facilitates the exploration of such bipartite networks. It provides functions to visualize networks and to calculate a plethora of indices to characterize network dynamics and the role of single species in a network.

Power and Stout (2011), who compared pollination networks on conventionally and organically managed pastures, stated that meadow management influences the structure of insect–flower interaction networks. Although the number of insect species was similar between networks of organically and conventionally managed pastures, significantly more plant species were visited within networks on organic farmland. The mean number of visited flowering plant species per insect species was higher there, which was the result of a higher proportion of generalist species in the insect community. Santos et al. (2012) suggested that Africanized honeybees (*Apis mellifera*) induce significant changes in the structure of native pollination networks in Brazil by occupying high functional dominance in networks. These few examples indicate that network studies have the potential to reveal important insights into the diversity and functioning of interactions between wild bees and the flowers they visit.

The aims of this study are:

1. To analyze relationships between bee-flower network metrics and habitat characters such as flooding, mowing regime or floral abundance.
2. To explore the influence of inundation on bee activity density and diversity. Based on available information on the responses of various insect groups to inundation (Fellendorf et al., 2004; Gerisch et al., 2012; Truxa & Fiedler, 2012; Fies et al., 2016) no well-founded assumption could be made about the potential effect of regular flooding. Nevertheless, it was still expected that at least the activity density of soil nesting bees would be lower on meadows which are flooded annually.
3. To compare the species composition of bee communities on meadows with, or without, annual inundations. Since the composition of bee communities is strongly altered by the properties of the environment the assumption was that there will be a distinct difference in species composition (Westrich, 1996).
4. To test what influence the abundance of the economically managed honeybee *Apis mellifera* has on the observed network metrics.

Material and methods

Study area

The National Park Donau-Auen is one of the last remaining natural floodplain systems in Central Europe. It stretches for 38 kilometers between Vienna and Bratislava (Arnberger et al. 2002) and covers an area of 9.300 (APA, 2016) ha, of which roughly 65% are floodplain forest, 20% are water and 15% are meadows. Due to its elongated shape the national park is less than 4 km wide at its broadest point which results in a strong interaction between the national park and the surrounding agricultural landscape (Nationalpark Donau-Auen GmbH, 2014).

Since the Danube, which flows through the national park, is a mountain river which is characterized by yearly flooding events, the proportion of average flow rate during low water and average flow rate during high-water is usually 1:6 (Michlmayr, 1997).

Centuries ago humans started to create meadows in the area by clearing parts of the floodplain forest. Since the building of the levee “Marchfeld-Schutzdamm” in the 1870ies, some of these meadows are no longer subject to the regular flooding regime, yet they persist due to extensive management (Nationalpark Donau-Auen GmbH, 2014). The actual mowing is done by contracted partners under control through the park administration and aims to preserve the meadows as a landscape-characteristic element of the area. Mowing is done twice a year except for some low-productivity sites which are mown just once a year (Nationalpark Donau-Auen GmbH, 2009).

Two main grassland types occur with regard to their inundation regime (Nationalpark Donau-Auen GmbH, 2009):

- Grassland that is flooded almost every year by the Danube and thereby fertilized by river sediments and dissolved nutrients.
- Grassland that is protected by the levee “Marchfeld-Schutzdamm” and therefore does not underlie regular flooding regime.

Therefore, meadows in the area vary differ concerning management (i.e. mowing frequency) and flooding regime, with flood-prone meadows being characterized by higher nutrient availability. These contrasts are further shaped by local topographical gradients, e.g. depending on elevation of the meadows in comparison to the Danube (Nationalpark Donau-Auen GmbH, 2009).

Study sites

Bee-flower networks on 32 meadows were recorded multiple times during late spring and summer 2016. Half of the meadows were situated north of the levee, while the other half was situated to the south. Since the summer flood in 2016 was exceptionally weak and consisted of only one, not exceptionally high peak which did not even last for 3 days, inundation did not disrupt the sampling efforts at all (DoRIS, 2016).

To facilitate comparisons with an earlier study on meadow butterflies (Fies, 2014), the 32 meadows sampled for this study were a subset of the 38 sites probed by her. The remaining 6 meadows were either deemed unsuitable because of severe management changes or represented a fraction of an already included meadow.

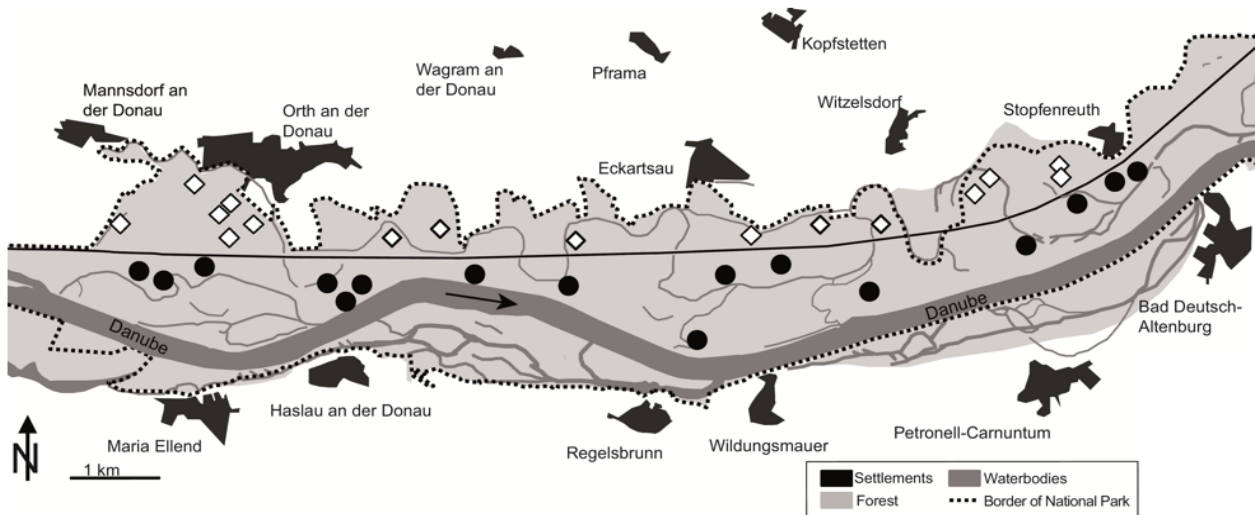


Figure 1. Map of the sampling area between Orth an der Donau and Stopfenreuth. Positions of the meadows are marked either with dots (south of the levee) or diamonds (north of the levee). The Map was provided by Fies et al. (2016) and modified.

Field Sampling

Sampling took place during 4 sampling periods between the end of April and the beginning of August. Each site was sampled for 30 minutes per survey. Bee sampling was carried out on 30 x 60 m plots in a central position on each meadow. Before sampling started, flowers that might serve as resources for bees were identified. Then, every flower on the plot was checked for bee-flower interactions. An interaction was defined as physical contact between the reproductive parts of a plant and a bee. When all flowers had been checked for interactions the sampling procedure was repeated until the 30 minutes had ended. Bees that could not be identified on the spot were captured with a net and transferred to snap cap vials prepared with ethyl acetate for later species identification in the laboratory. Because of their distinct appearance and feeding habits, which allow a precise identification of living individuals, the two highly specialized species *Andrena hattorfiana* and *Chelostoma florissomne* were determined in the field, documented, and released.

Sampling was only performed if weather conditions were deemed adequate to meet a sufficient number of bees in the field. Accordingly, sunny weather, lack of strong wind and daytime between 9:30am and 4pm were required for the sampling process to take place.

The plant species on which each bee had been collected was recorded, identified after Fischer et al. (2008) and assigned to its observed flower visitor. To facilitate identification, vouchers of the collected bees were arranged and stored according to standard entomological techniques as described by Ebmer (2010). Bees were identified using a stereo-microscope and appropriate literature, in some of the more difficult cases with the assistance of Dr. Bärbel Pachinger of the University of Natural Resources and Life Sciences in Vienna.

Data Acquisition

To test for the impact of inundation the meadows were separated into two groups: meadows north of the levee and meadows south of the levee. For all sampled meadows except of one, plant species lists were provided by the national park administration. If applicable the list of flowering plants acquired during this study was used for the one meadow which lacked a vegetational description. The abundance of flowering plants which could serve as potential food sources for bees was valued on a rank scale of 1 to 5 before sampling. 1 represented a very low, 5 an exceptionally high floral abundance. It was also recorded if the meadow had been mown since the last sampling took place.

All honeybee (*Apis mellifera*) – plant interactions were also recorded. If there were too many honeybees on one site to document them easily while sampling wild bees, the number of honey bee – plant interactions was estimated. This was the case on 2 sampling events.

To test if the position of a site relative to the levee had an influence on the total numbers and proportions of soil nesting bees, bee species were classified as either soil-nesting or non-soil-nesting using the classification by Scheuchl and Willner (2016) The category “not soil nesting bees” also includes bees which frequently nest in soil but are able to use non-terrestrial nesting substrate like old wood or stems of annual herbs.

Network Analysis

All recorded interactions were transformed into one data matrix containing all interactions observed during the 4 sampling periods across all sites, and into 32 individual matrices containing only the interactions observed on single meadows. Network metrics and figures regarding the network analysis were generated using the R package “bipartite” (Dormann et al., 2016). To visualize the whole dataset in a bipartite graph the function “plotweb” was used.

The interaction webs of individual meadows were characterized by quantitative network parameters using the ‘networklevel’ function in the bipartite package (Dormann et al., 2016). Qualitative foodweb parameters were completely omitted because they are much more influenced by sampling effort than their quantitative counterparts, which weigh interactions according to their frequency. Since the dataset is rather small the probability of a bias when using qualitative parameters appeared too likely (Bersier et al., 2002; Banašek-Richter et al., 2004; Blüthgen et al., 2008; Power and Stout, 2011).

From the large list of available network metrics, I selected the following for further analysis:

1. $H2'$: A network-level measure of specialization, based on the deviation of a species' realized number of interactions and that expected from each species' total number of interactions. The resulting $H2'$ ranges between 0 (no specialization) and 1 (perfect specialization for given interaction totals; Dormann et al., 2009).
2. Vulnerability: Weighted linkage for plants, calculated as the weighted mean number of insect visitor taxa per plant species (Tiedeken et al., 2015).
3. Niche overlap for higher trophic level: Mean similarity in interaction pattern between species of the same trophic level. Values near 0 indicate no common use of niches, 1 indicates perfect niche overlap (Dormann et al., 2009).

To assess which species play an exceptionally important role in the networks of the national park the network metric “species strength” was calculated for bee species from two aggregated datasets: one for northern and one for southern meadows. The strength of a bee species is defined as the sum of dependencies of the plants relying on this bee. This means it is a measure of importance of a bee species from the perspective of the flowering plant species set. This measure is a quantitative extension of species degree, which is the number

of interactions per species in qualitative networks (Bascompte et al., 2006). For further exploration of the dynamics behind the species strength index I tested (two separate GLMs) how strong the number of observed individuals of each bee species was related to its number of visited plant species and actual species strength.

Statistical Data Analysis

Statistical analysis was performed using R Studio, which is an integrated development environment (IDE) for R (R Core Team, 2013; RStudio Inc., 2016). To compare species richness between the bee communities north and south of the levee, individual-based and sample site-based species accumulation curves were calculated using the package “iNEXT” (Chao and Hsieh, 2016). For the sample-site-based species accumulation curve regarding the number of wild bee species, extrapolation to the factor 2.19 was necessary to obtain a clear result.

To test for relationships between site descriptors and response variables pertinent to the bee-flower networks, Generalized Linear Mixed Models (GLMMs) as implemented in the “lme4” package (Bates et al. 2016) were performed. Hence each meadow was represented by 4 individual sampling events and in all calculated GLMMs the meadow-ID was set as random factor.

The first two GLMMs tested if the position of sites relative to the levee (two categories), flower density, and number of plant species visited by wild bees had an effect on the observed bee activity density and observed number of bee species. To prevent an excess of multicollinearity in the models, the influence of mowing (if the meadow had been mown since the last sampling effort) on wild bee activity density and species numbers was tested separately.

To determine whether the position relative to the levee and mowing status influenced the numbers of soil nesting or non-soil nesting bees, and if the same two predictors influenced the number of oligolectic and polylectic bees, further GLMMs were calculated. Because of the special status of *Lasioglossum marginatum*, another GLMM was calculated to test if inundation exposure had an influence on the individual numbers of this particular focal species.

Two Linear Mixed-Effects Models were calculated to test how the proportion of oligolectic bees and the proportion of non-soil nesting bees (both logit transformed) responded to the mowing status and the position relative to the levee. Another Linear Mixed-Effects Model tested if the environment south of the dam favors bees which show a preference for cool and humid habitats. To identify species of this sort, classification by Pittioni & Schmidt, 1942; Pittioni & Schmidt, 1943 and Pachinger et al., 2014 was used.

The three network metrics vulnerability, H2 and niche overlap were calculated for each meadow separately, using the accumulated interactions of all 4 sampling events. In another set of GLM analyses it was tested if the three network metrics were influenced by the position relative to the levee, mowing status (in this case if the meadow was mown at all between one of the sampling events), accumulated number of all visited flower species on a meadow and proportion of polylectic bee individuals. The latter two predictors were chosen because the extent of specialization is predicted to have a major effect on most network metrics (Dormann et al. 2016). All metrics except of vulnerability (which was log transformed) were logit transformed.

To simplify the general linear models I applied a classical model selection approach using forward selection based on the small-sample-size corrected version of Akaike information criterion (AICc). Predictors which were removed during model selection will also be omitted in the results.

To visualize if the position of sites relative to the levee, the number of vascular plant species according to vegetation lists and actual flower density influenced bee species composition, a Bray-Curtis dissimilarity matrix containing samples from all 32 meadows was created. Based on this data a Constrained Analysis of Principal Coordinates (CAP) was computed using the function `capscale` implemented in the package "VEGAN" (Oksanen et al. 2017). In addition, an ANOSIM, which is also implemented in the package "VEGAN" (Oksanen et al. 2017), was computed, also testing for effects of flooding on the bee species composition.

To determine if the position of meadows relative to the dam affected bee and plant differentiation diversity respectively, a permutation-based multivariate analogue of Levene's test for homogeneity of variances with 1000 permutations was performed. The procedure is implemented in the package "VEGAN" (Oksanen et al. 2017). For analyzing bee differentiation diversity, the abundance based Bray-Curtis index was used, while for the qualitative data of

the plant species lists the incidence-based Jaccard index was used. Although Anderson et al. (2006) proposed that differences in beta diversity among different areas or groups of samples can be tested using this approach, Tuomisto (2010) criticized the wide variation of compositional heterogeneity phenomena which were all referred to as “beta diversity” and offered more clear nomenclature approaches, in this particular case namely differentiation diversity.

Results

A total of 686 wild bee individuals were recorded over all four sampling periods. Since some of the bees performed more than one interaction with flowers before being caught, the number of wild bee × flower interaction was slightly higher.

1103 bee-flower interactions were recorded of which 393 included honeybees, and 710 wild bees. Honeybees appeared at only 28 sampling events but during some of them in great numbers. Of the 1103 interactions 272 were unique interactions, representing a unique bee × plant species pair.

During the survey interactions of 61 flowering plant species with 92 wild bee species from 19 genera were recorded. With 223 interactions *Bombus* was the wild bee genus with the most interactions. The species responsible for the highest number of interactions was *Chelostoma florisomne* which is exclusively specialized on flowers of the plant genus *Ranunculus*.

On the meadows north of the levee a total of 61 wild bee species and 413 flower interactions were recorded. North of the dam 34.7% of all observed wild bees were soil nesting individuals. On the southern meadows 71 wild bee species and 297 interactions were recorded, here 42.7% of observed wild bees were soil nesting.

Furthermore, 43 *Lasioglossum marginatum* individuals were recorded on 11 northern meadows compared to only 10 individuals on 7 southern meadows.

Species accumulation curves

Both individual based and sample site based species accumulation curves paint a clear picture: contrary to expectation wild bee species richness was significantly higher on flood-prone meadows south of the levee.

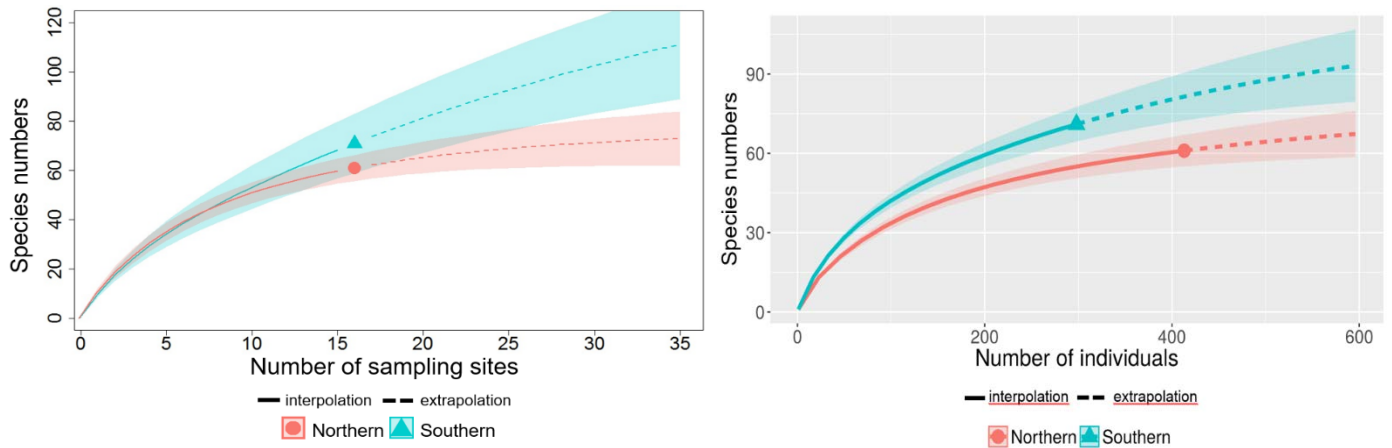


Figure 1. Sample site based (left) and individual based (right) randomized species accumulation curves of wild bee species numbers north and south of the levee. The shaded areas represent 95% confidence intervals.

Wild bee activity density and species numbers

Wild bee activity density was significantly positively correlated to estimated floral abundance and number of visited plant species (Table 1). A significantly higher activity density was found on meadows which had not been mown since the last survey. The position of the meadows north or south of the dam showed no significant effect at all.

The observed number of wild bee species per meadow showed a similar picture as the wild bee activity density: a highly significant positive correlation to the number of visited flower species and floral abundance was found. The mowing status also had an influence on species numbers, significantly more species were found on meadows that had not been mown since the last survey. The position relative to the levee had no significant effect at all.

Table 1. Results of generalised linear mixed models, testing the effects of selected predictors on wild bee activity density and the number of observed bee species. Significant effects ($p < 0.05$) printed in bold.

Dependent variables	<i>marginal R²</i>	<i>conditional R²</i>	Explanatory variables	<i>z</i>	<i>p</i>
Wild bee activity density	0.713	0.730	Position	-1.334	0.182
			Visited plant species	2.891	0.004
			Floral abundance	13.138	<0.001
Wild bee species number	0.622	0.622	Position	0.451	0.650
			Visited plant species	4.474	<0.001
			Floral abundance	7.914	<0.001

Table 2. Results of generalised linear mixed models, testing the effects of mowing status on wild bee activity density and the number of observed bee species. Significant effects ($p < 0.05$) printed in bold.

Dependent variables	<i>marginal R²</i>	<i>conditional R²</i>	Explanatory variables	<i>z</i>	<i>p</i>
Wild bee activity density	0.563	0.563	Mowing	-8.901	<0.001
Wild bee species number	0.501	0.519	Mowing	-6.575	<0.001

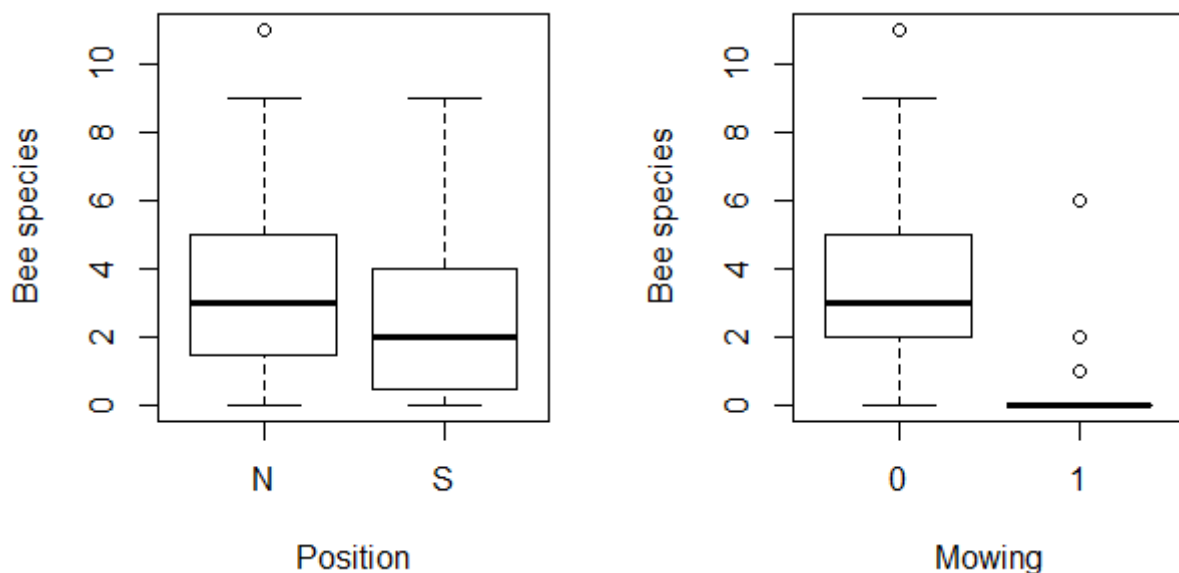


Figure 3. Number of observed wild bee species relative to the position relative to the levee (right) and the mowing status (left). Box-and-whisker-plot, range = 1.5 * IQR. N = North of the dam, S = South of the dam, 0 = not mown since the last survey, 1 = mown since the last survey.

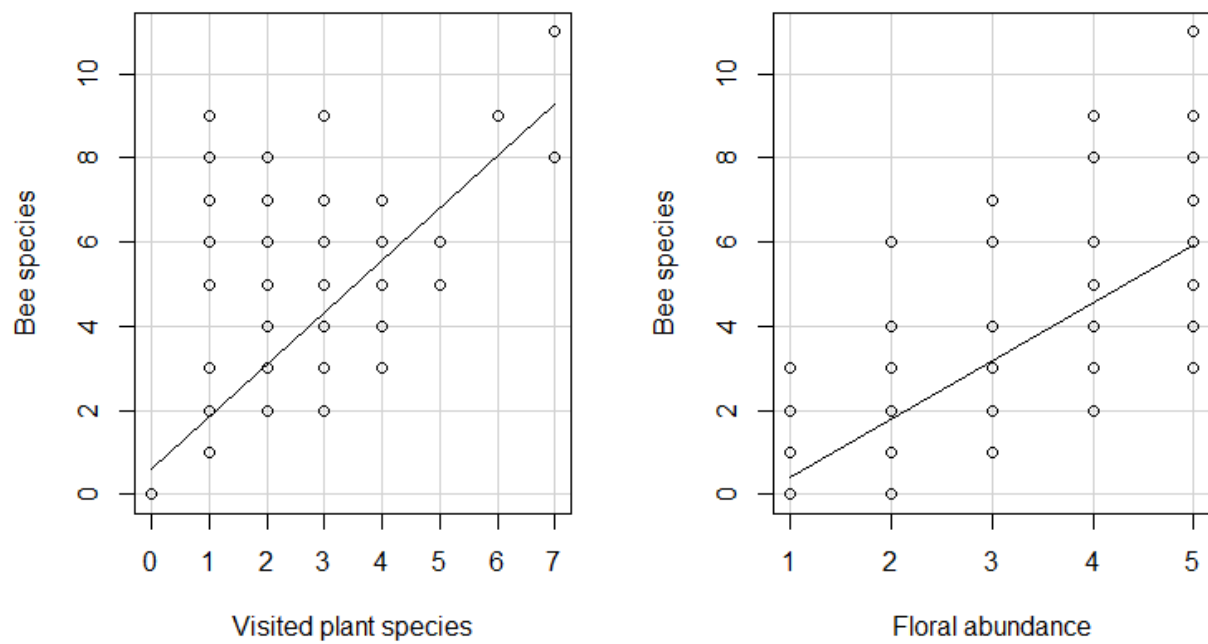


Figure 4. Scatterplots showing the relationship between number of visited plant species and number of observed bee species (left) and the relationship between floral abundance and number of observed bee species (right).

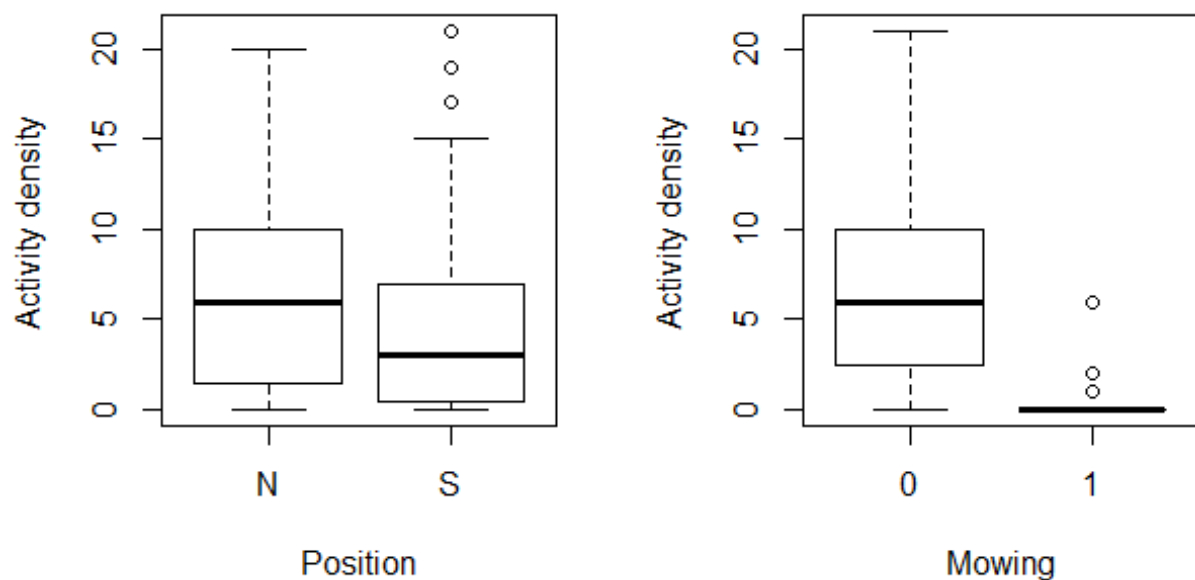


Figure 5. Observed wild bee activity density relative to the position relative to the levee (left) and the mowing status (right). Box-and-whisker-plot, range = $1.5 \times \text{IQR}$. N = North of the dam, S = South of the dam, 0 = not mown since the last survey, 1 = mown since the last survey.

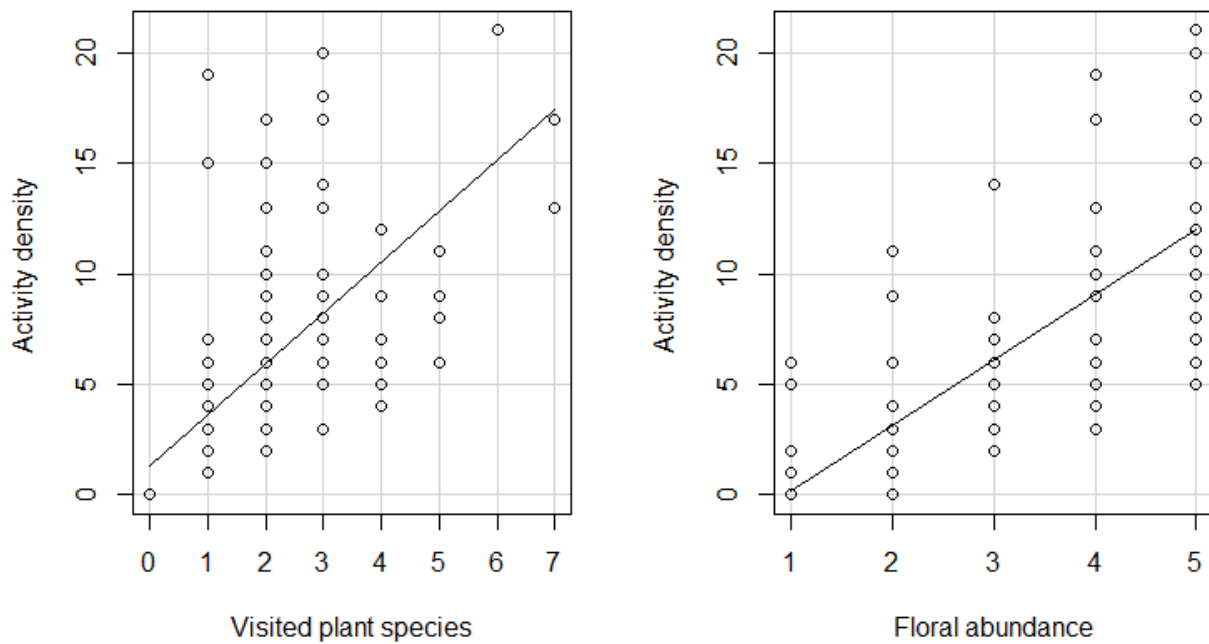


Figure 6. Scatterplots showing the relationship between number of visited plant species and activity density (left) and the relationship between floral abundance and activity density (right).

Nesting preferences and oligolecty

Neither the observed proportion of non-soil nesting bees nor the proportion of oligolectic bees was significantly influenced by the position relative to the levee or the mowing regime.

Nevertheless, the total number of observed non-soil nesting bees was significantly higher on northern meadows and on meadows that had not been mown right before my surveys. Mowing also had a significantly negative effect on numbers of soil nesting bees.

Concerning nutritional preferences, significantly more oligolectic bees were found on meadows situated north of the dam and significantly more polylectic and oligolectic bees were found on meadows which were not shortly mown.

Furthermore, no significant correlation between tested proportion of bees which show a preference for cool and wet habitats and the position relative to the levee could be determined.

Table 3. Results of generalised linear mixed models, testing the effects of position relative to the levee and mowing status on activity density numbers of selected species groups. Significant effects ($p < 0.05$) printed in bold.

Dependent variables	<i>marginal R²</i>	<i>conditional R²</i>	Explanatory variables	<i>z</i>	<i>p</i>
Soil nesting bees	0.375	0.375	Position	-0.454	0.65
			Mowing	-5.960	<0.001
Non-soil nesting bees	0.443	0.443	Position	-2.938	0.00331
			Mowing	-6.607	<0.001
Polylectic bees	0.445	0.445	Position	-1.215	0.224
			Mowing	-7.637	<0.001
Oligolectic bees	0.938	0.938	Position	-2.535	0.0112
			Mowing	-0.150	<0.001

Table 4. Results of generalised linear mixed models, testing the effects of position relative to the levee and mowing status on the proportional activity density of selected species groups. Significant effects ($p < 0.05$) printed in bold.

Dependent variables	<i>marginal R²</i>	<i>conditional R²</i>	Explanatory variables	Chisq	Df	<i>p</i>
Prop. non-soil nesting bees	0.007	0.056	Position	0.21	1	0.647
			Mowing	0.358	1	0.55
Prop. oligolectic bees	0.04	0.04	Position	0.087	1	0.768
			Mowing	3.733	1	0.053
Preference for humid habitats	<0.001	0.125	Position	0.018	1	0.8925

Lasioglossum marginatum

Although inundation exposure did not have a significant influence on the sheer occurrence of *Lasioglossum marginatum*, significantly fewer individuals were found on the southern meadows ($z = -2.553$; $p = 0.010$; $mR^2 = 0.008$; $cR^2 = 0.008$).

Flower diversity and abundance

The number of visited flower species per site was significantly higher on northern meadows ($z = -2.338$, $p = 0.0194$; $mR^2 = 0.047$; $cR^2 = 0.049$). However, the total number of visited flower species aggregated over all southern meadows was barely smaller than north of the dam

(North: 47, South: 41 flower species) and the number of visited flower species per observed individual bee was actually higher on meadows south of the levee (North: 0.11, South: 0.14). In terms of floral abundance there was only marginal difference between the two meadow categories (Average floral abundance north of the levee: 2.92; south of the levee: 2.72).

Network metrics

Position of meadows relative to the levee and number of interactions in the networks did not have a significant effect on any of the tested network metrics on the level of individual meadows. Vulnerability significantly increased with the proportion of polylectic wild bees and significantly decreased with increasing honeybee interactions in the networks.

After automatic model selection for H2' the only remaining predictor in the GLM was “Visited flower species” which showed that H2' significantly decreased with increasing number of flowering plant species actually represented in the networks.

Niche overlap of bee species was positively related to the proportion of polylectic bees and negatively correlated to the number of visited flower species.

Table 5. Results of general linear models, testing the effects of the predictors position, visited plant species, mowing regime, proportion polylectic and abundance of *Apis mellifera* on bee × flower network metrics. Additionally pseudo-R² after Nagelkerke and mean (±SE) network parameter values of all meadows together are given. Only effects that remained after automated model selection in the simplified models are shown. Significant effects ($p < 0.05$) are printed in bold.

Dependent variables	Mean ± SE	R ²	Explanatory variables	<i>t</i>	<i>p</i>
Vulnerability	2.57 ± 0.25	0.54	Proportion polylectic	3.987	<0.001
			<i>Apis mellifera</i>	-2.305	0.023
H2'	0.80 ± 0.03	0.16	Visited plant species	-2.369	0.025
Niche overlap	0.25 ± 0.04	0.6	Visited plant species	-5.723	<0.001
			Proportion polylectic	2.92	0.007

Important players in the networks

Network analysis revealed a far more pronounced species strength of *Apis mellifera* on the southern meadows, where the honeybee was actually the species with highest strength (on

northern meadows only rank 13, in contrast). *Bombus pascuorum* played a central role in both areas with by far highest species strength on northern meadows and the third highest species strength south of the levee. *Lasioglossum marginatum* showed an exceptionally high species strength on the northern meadows which was more than double of that on the southern meadows. *Lasioglossum calceatum* played a minor role in the northern network, but had the second highest species strength in the southern network. To sum up, there were numerous bee species which played a significant role in both networks but the main players often differed between flood-prone and non-flooded meadows.

The number of observed individuals per bee species correlated significantly with both, the diversity of plant species visited by each species ($t = 6.121$, $p < 0.001$) and the actual species strength values ($t = 5.531$, $p < 0.001$).

Table 6. The 10 most important players in the bee × flower networks north and south of the levee, according to the network metric “species strength”.

Northern Network		Nr.	Southern Network	
Species name	species strength		Species name	species strength
<i>Bombus pascuorum</i>	9.81	#1	<i>Apis mellifica</i>	7.12
<i>Lasioglossum marginatum</i>	3.40	#2	<i>Lasioglossum calceatum</i>	3.59
<i>Bombus humilis</i>	1.97	#3	<i>Bombus pascuorum</i>	2.56
<i>Lasioglossum laevigatum</i>	1.96	#4	<i>Lasioglossum zonulum</i>	2.23
<i>Bombus sylvarum</i>	1.78	#5	<i>Halictus subauratus</i>	1.74
<i>Halictus subauratus</i>	1.67	#6	<i>Hylaeus communis</i>	1.66
<i>Chelostoma florisomne</i>	1.63	#7	<i>Bombus sylvarum</i>	1.56
<i>Andrena ovatula</i>	1.50	#8	<i>Chelostoma florisomne</i>	1.56
<i>Heriades truncorum</i>	1.32	#9	<i>Lasioglossum pauxillum</i>	1.52
<i>Hylaeus communis</i>	1.25	#10	<i>Lasioglossum marginatum</i>	1.45

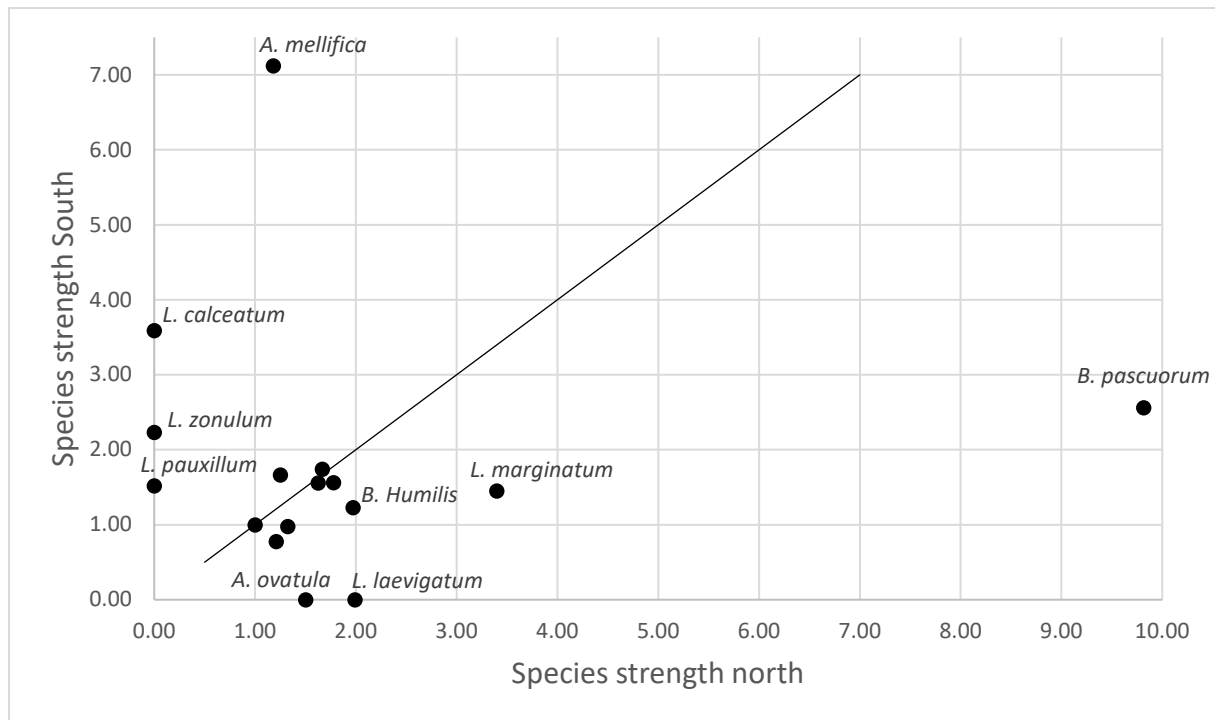


Figure7. Scatterplot showing the species strength of the 16 strongest Species for meadows situated north and south of the levee. Players that differ exceptionally strong between the two meadow categories are labelled.

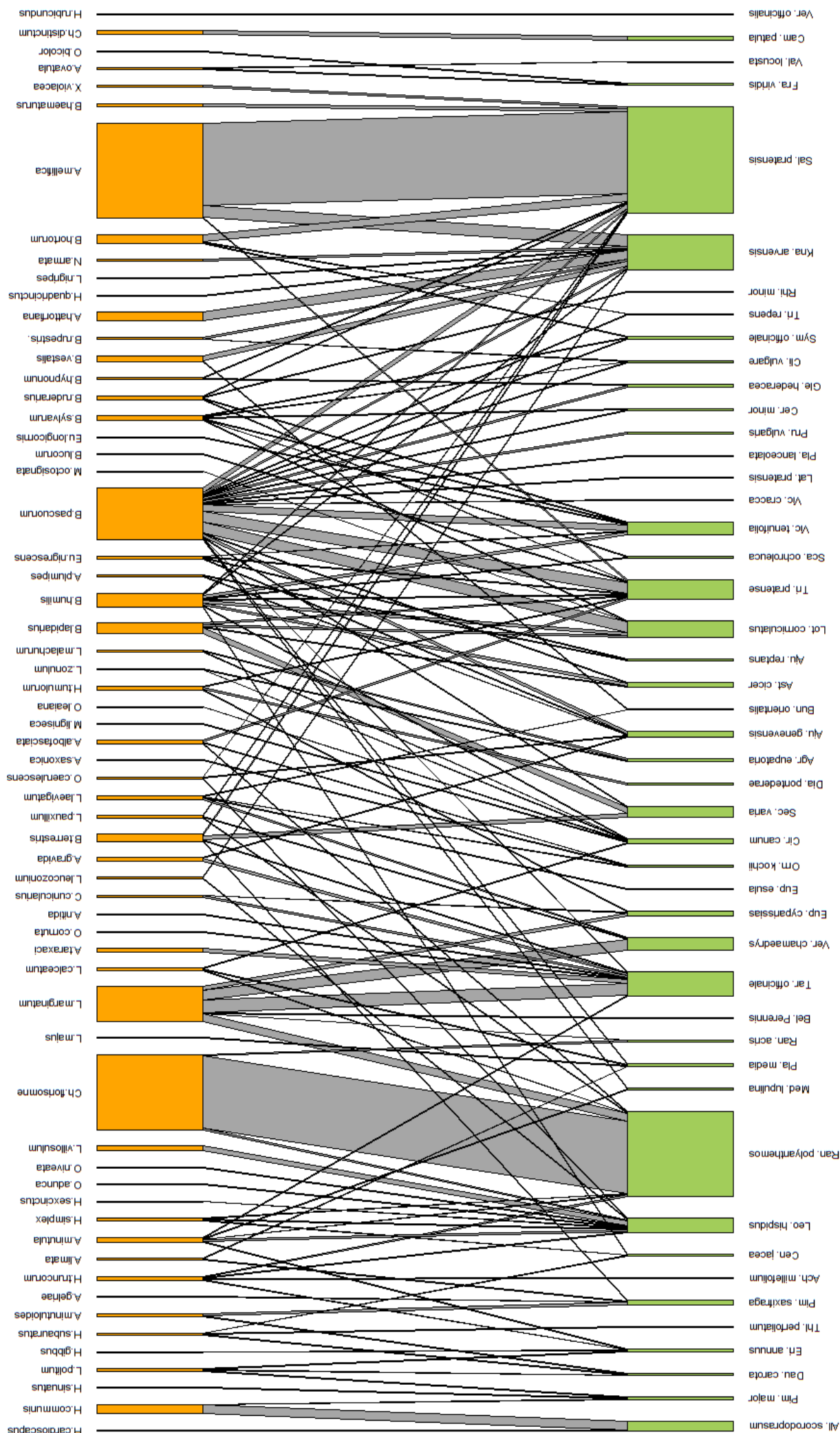


Figure 8. Bipartite graph of the bee x flower network aggregated over all 16 northern meadows. Wild bees in orange, plants in green. The thickness of the bars connecting the two trophic levels reflects the number of observed interactions. *Bombus pascuorum* which visited a broad spectrum of different plant species plays a central Role in this network. *Apis mellifica* interacted predominantly with *Salvia pratensis*.

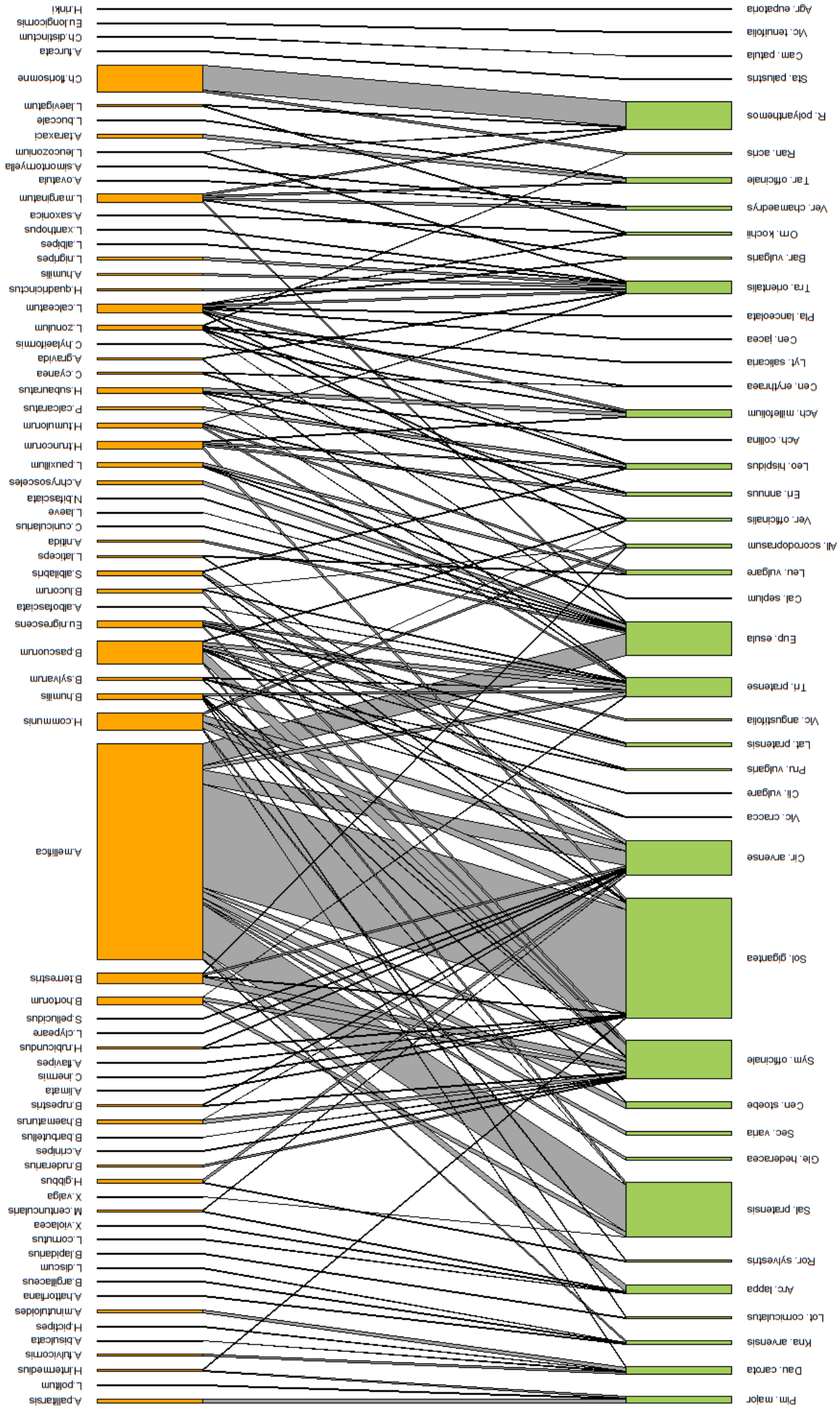


Figure 9. Bipartite graph of the bee x flower network aggregated over all 16 southern meadows. Wild bees in orange, plants in green. The thickness of the bars connecting the two trophic levels reflects the number of observed interactions. By contributing 45.9% of all interactions and visiting a broad spectrum of different plant species, *Apis mellifera* plays a very dominant role in this network, resulting in the highest species strength of all bee species.

Species composition

A Canonical Analysis of Principal Coordinates (CAP) showed a clear separation of the data points representing the individual bee communities. Notably the vectors indicating “Position” and “Total plant species richness” show in almost opposite directions while “Floral abundance” lies almost orthogonal to the other 2 predictors. Even though the model explained only 14.37% ($R^2_{\text{adjusted}}: 5.2\%$) of the total variability in bee species composition between the meadows, the clear separation of data points on the plot suggests that the 3 predictors play important roles in shaping the species composition of the bee communities (Anderson & Willis, 2003). When the effect of flooding on species composition was tested individually with an ANOSIM, the influence was significant but weak ($R = 0.092$, $p=0.021$).

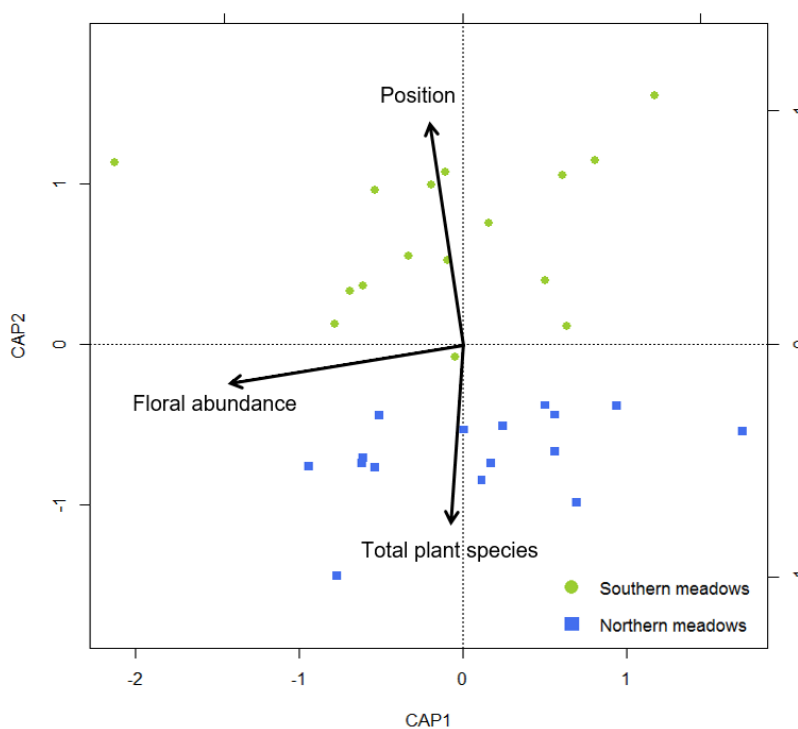


Figure 10. Constrained ordination plot from a Canonical Analysis of Principal Coordinates (CAP) based on a Bray Curtis dissimilarity matrix containing bee assemblages from all 32 meadows. Three vectors were used to span out communities in reduced ordination space.

The Bray-Curtis dissimilarity based analyses revealed a significantly higher heterogeneity ($Df=1$, $F= 7.556$, $p= 0.001$) of wild bee communities on the meadows south of the levee than on northern meadows. Heterogeneity of plant communities based on Jaccard dissimilarities was only marginally, and not significantly, higher ($Df= 1$, $F= 2.9588$, $p= 0.0751$) on meadows south of the levee.

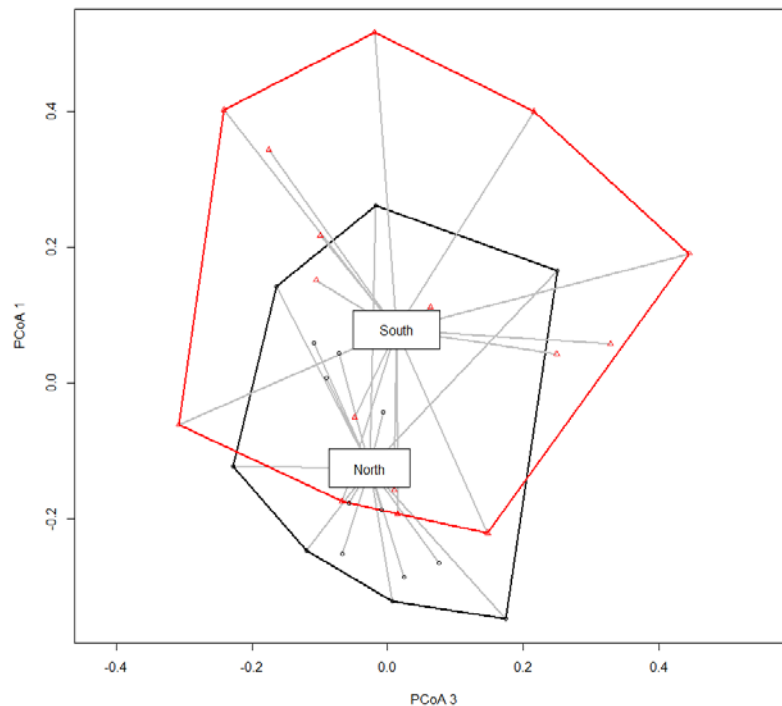


Figure 11. Visualization of 1st and 3rd Bray-Curtis dissimilarity based PCoA Axes, depicting differentiation diversity of Bees on northern and southern meadows. Increased differentiation between the meadows leads to higher dispersion of the data points.

Rare or otherwise remarkable species

Andrena bisulcata

In central Europe this species was so far only found in the Pannonian part of Austria. Before Dr. Pachinger (2002) rediscovered this bee species in the year 2001 in Spillern (Lower Austria), the last time it had been recorded in Austria was in 1938. Why this species was not found for such a long period remains unclear (Pachinger, 2012). Schmiedeknecht (1930) still refers to this species as exclusively specialized on the plant genus *Apiaceae* whereas Scheuchl and Willner (2016) described it as “potentially polylectic”. One single individual was caught on a meadow south of the dam while interacting with *Daucus carota*.

Andrena pallitarsis

All 5 individuals of this relatively rare species were found on one meadow south of the dam, interacting with the plant *Pimpinella major*. It is specialized on the plant genus *Apiaceae* as pollen source (Scheuchl and Willner, 2016).

Andrena saxonica

This bee species is specialized on the plant genus *Ornithogalum* (Scheuchl and Willner, 2016). Both caught individuals (one north and one south of the dam) were found while feeding on *Ornithogalum kochii*, which is classified as threatened in Austria (Fischer et al., 2008).

Anthophora furcata

This arboreal species is relatively rare in Austria. As feeding source it is exclusively specialized on the plant genus *Lamiaceae*, with a special preference for plants of the subgenus *Stachys*. Its dependence on dead wood structures as nesting substrate let it disappear in many too intensively managed forest regions (Pachinger, 2002). A single individual was found on a southern meadow while feeding on *Stachys palustris*.

Chelostoma florisomne

Chelostoma florisomne was by far the most abundant bee species. As pollen source it is strictly specialized on the plant genus *Ranunculus*. As *Ranunculus* is a relatively common plant genus in Austria, the limiting factor for this bee species is usually the availability of appropriate nesting sites which are directional cavities, usually in dead wood structures or hollow stems of herbs. Although this species is not remarkably rare its mass occurrence is still remarkable (Pachinger, 2002; Fischer et al., 2008; Scheuchl and Willner, 2016). The extensively managed floodplain forest seems to provide optimal nesting resources for this species.

Hylaeus cardioscapus

This rare species is almost exclusively found in floodplain areas. As nesting habitat it uses cavities in dead wood or hollow stems of herbs (Scheuchl and Willner, 2016). One single individual was found on a meadow situated north of the dam which is situated directly next to an abandoned meander, which is flooded when the Danube is in high flood.

Lithurgus cornutus

So far, there are only two other places in Lower Austria where this rare bee species was found. Both of these places are situated in the floodplain area of the Danube. As pollen source this oligolectic species is specialized on plants of the subgenus *Carduoideae*. As nesting substrate it uses dead wood (Pachinger, 2012; Scheuchl & Willner, 2016). Only one individual was found on one of the southern meadows which apparently has not been mown over the last 2 or 3 years, while feeding on *Arctium lappa*.

Megachile octosignata

In central Europe this bee species was only found in Austria so far (recent findings only in Lower Austria and Burgenland) and here only extremely seldom. It is classified as potentially polylectic with a preference for plants of the genera *Fabaceae* and *Asteraceae*, nests in cavities in old wood or stone and is bound to dry and hot habitats (Zettel et al., 2009; Scheuchl and Willner, 2016). A single individual was found on a meadow south of the dam, feeding on the plant *Lotus corniculatus*.

Discussion

General bee richness and activity density

92 wild bee species were found in total, which equals 15.33% of the total Lower Austrian wild bee fauna (Schwarz et al. 2005). Still, steep species accumulation curves, especially for the southern meadows, suggest that there are many species left which were not captured during the survey. These findings correspond to former surveys which were performed in Western Austria where species numbers usually ranged between 90 and 150 species (Pachinger, 2002; Pachinger & Hölzler, 2006; Ockermüller & Zettel, 2013; Pachinger et al., 2014). In respect of the sampling effort, 686 recorded bee individuals are not an exceptionally high number (Pachinger et al., 2014). A possible explanation for the relatively low individual numbers may be the extremely humid weather from April to August, with two to three times as much precipitation as usually and a precipitation all-time record for June (ZAMG, 2017). Both, floral abundance and, closely related to that, mowing had a highly significant influence on the wild

bee activity density. The positive correlation of bee abundance and floral abundance was already described by Steffan-Dewenter & Tscharnkte (2001) and Potts et al. (2003). The number of observed bee species also showed a highly significantly positive correlation to floral abundance. Holzschuh et al. (2007) found the same connection and concluded that, provided that a certain threshold of plant diversity is exceeded, high floral abundance may promote a species rich bee community although this community will be dominated by pollen generalists.

Effects of flooding

Although more species were recorded on northern meadows and mean number of bee species per site was even slightly lower south of the dam (North: 11, South: 10), species accumulation curves indicate an overall higher species richness aggregated over all southern, annually flood-prone meadows. This is surprising since at a first glance one would expect wild bees, especially those nesting in or near the ground, to be particularly susceptible to mortality through inundation episodes. The finding also stands contrary to a higher butterfly richness on non-flooded meadows that Fies et al. (2016) found in the years 2012 and 2013 (a year in which notably severe flooding occurred). They concluded that the southern meadows house a lower number of butterfly species because the flooding reduces the abundance and consequently the species number. Truxa and Fiedler (2012) who investigated forest moth communities in relation to flood regime across three riparian forest regions in lowland eastern Austria (one of them was the alluvial forest of the National Park Donau-Auen) revealed no general negative impact of flooding on the diversity and species composition, they even found a slightly richer moth fauna on flooded habitats of the National Park Donau-Auen.

A potential explanation for higher bee richness south of the dam could be the significantly higher bee species turnover between sites. Pollock et al. (1998) who surveyed plant species richness in riparian wetlands in southeast Alaska described that against expectations an extremely high variation of flood-disturbance regime in an area only as small as 1000 m² was found. The described variation was mainly caused by microtopographic variation. It seems reasonable to assume a similar variation to exist for the meadows south of the dam in the National Park Donau-Auen as some of them lie on a higher elevation than others, which are situated directly alongside the Danube. As a consequence, elevation-related flooding

represents a very strong gradient on these meadows. It is widely known that the degree and regularity of inundation events have a strong influence on the species composition of plant communities (Hupp, 1983; Bornette & Amoros, 1996; Van Looy et al., 2003). Van Looy et al. (2003) studied the effects of disruption of alluvial forests from river flooding on their vascular plant diversity in the river Meuse floodplain in Belgium. They found a significantly higher plant beta diversity in forests still under influence of a regular flooding regime.

What could corroborate the hypothesis of higher differentiation diversity south of the dam is that although the number of flowering plant species visited by wild bees per meadow was significantly lower on the southern meadows (i.e. the concentration on fewer flower species was more pronounced), the total number of visited flower species was only marginally smaller (North: 47, South: 41) and the number of visited plant species per observed individual bee was actually higher (North: 0.11, South: 0.14) on the meadows south of the levee. Since the composition of the surrounding vegetation is one of the top factors altering the assembly of bee communities (Westrich, 1996; Ebeling et al., 2008) it seems likely that an increased plant beta diversity was one of the reasons for high bee species turnover and, accordingly, species numbers south of the levee. When Żmihorski et al. (2016) observed a significantly higher beta diversity and species richness of birds on flooded grassland areas compared to non-flooded areas in Sweden, they also concluded that this effect may have been driven by the more heterogeneous vegetation structure on regularly flooded sites. Gerisch et al. (2012) found an exceptionally high beta diversity of ground beetles on meadows experiencing frequent inundation and thereby showed that this concept is also applicable for terrestrial invertebrates. Former studies in the national park point in different directions: whereas ordination plots of butterfly communities by Fies et al. (2016) suggest a higher heterogeneity south of the dam, no such effect was found by Truxa & Fiedler (2012) and Demetz et al. (2013). Since Fies et al. (2016) and I used almost concordant sampling sites, it seems possible that the matching results are the consequence of this methodical overlap.

Another potential driver of bee species richness south of the dam could have been the different habitat dynamics. The strong elevation-related flooding gradient could have led to a more fine-grained habitat structure providing more different succession stages and microhabitats (Pollock et al., 1998). The same relation was found by Vivian-Smith (1997) who tested in an experimental design whether the diversity of wetland plant communities was

associated with small-scale spatial microtopographic heterogeneity in experimental wetland communities: Floristic diversity and species richness were consistently greater in communities with heterogeneous microtopography. This case emphasizes the basic principles of the widely known “habitat heterogeneity hypothesis” which assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity. In a meta-analysis performed by Tews et al. (2004) 85% of all 85 surveyed studies found a positive correlation between species diversity and habitat heterogeneity. As variation in duration of flooding is an important factor maintaining species diversity in plant communities (Vivian-Smith, 1997; Lenssen et al., 2004) the same can be true for certain groups of animals and particularly terrestrial insects (Gerisch et al. 2012; Truxa & Fiedler, 2012; Żmihorski et al. 2016). Additionally, based on subjective memory, more potential nesting habitats such as bare patches on the meadows, obviously caused by activities of wild boars during wet periods, were observed south of the levee. Since wet soil facilitates activities like rooting and wallowing, wild pigs preferably frequent marshes and wetlands (Dardaillon, 1986). Wild hogs can have substantial influence on the structure of floodplain vegetation assemblages leading to reduced plant cover and to significantly higher microhabitat diversity and species richness (Arrington et al., 1999). Hence wild boars are often referred to as “ecosystem engineers” (Pankova, 2013). Combining the facts that many bee species depend on open sun-exposed patches as nesting habitat and the general high dependency of bees on the local flora, (Westrich, 1996; Zurbuchen & Müller, 2012) it appears likely that the activities of wild boars may have a positive effect on the structure of local wild bee assemblages.

I want to point out that the potentially high degree of undersampling and associated with it, the high number of singletons and doubletons may have led to a certain overestimation of species turnover. Notably the proportion of bees that were in common to northern as well as southern meadows was only 36.8%. Since the meadows south of the dam were even more undersampled than the northern meadows, the difference in species turnover between the two meadow categories could be mitigated when comparing more complete datasets (Beck & Schwanghart, 2010; Beck et al., 2013). Furthermore bee communities are known for exhibiting substantial variation over space and time. Bee faunas, even of local areas often appear diverse. This highly dynamic property of bee populations and their local diversity may also have served as leverage for local species turnover (Williams et al., 2001).

The data suggests a high resilience of bee communities to flooding events. Gerisch et al. (2012), who investigated the impacts on ground beetles of an unpredictable catastrophic flood event of the Elbe River in Germany in the year 2002 using pre- and post-flood data, found that species richness and abundances decreased strongly immediately after the flood. Less than 50% of the species and only 20% of the individual numbers were sampled right after the flood. Nevertheless, pre-flood values were restored only two years later. They concluded that ground beetles show low resistance but high resilience to extreme flooding events and explained this resilience with reproductive traits and high dispersal power of beetles. Especially regarding wild bees, Fellendorf et al. (2004) observed a massive population decline of two aggregations of *Andrena vaga* after a flooding event in May 1999 at the river Rhine. This suggests that flooding events may have similar disastrous effects, at least on assemblages of soil nesting bees. Furthermore Küpper (2017, personal communication) who observed bumblebees in alluvial regions of the Lobau, reported recurrent population declines following severe flooding events. Hence bees which are not exclusively soil-nesting (as most bumblebees are) also seem to be heavily affected by floods.

Interestingly, more pollen-specialist bees were found on meadows situated north of the dam. Strong environmental fluctuations favor high dispersal and thus act against local adaptation. In contrast, spatial environmental heterogeneity facilitates reduced dispersal and habitat fidelity, which make conditions for local adaptation more favorable (Kisdi, 2002; Kawecki & Ebert, 2004). Hence it is comprehensible that the more stable environment north of the levee promoted species with a higher degree of nutritional specialization.

The last extreme flooding event of the Danube in 2013 occurred with a severity estimated to take place only once every 200 years. During the following years, including the year in which this study was performed, floods were particularly weak (Land Niederösterreich, 2017). Since bee individuals from local communities in more flood protected areas (presumably north of the dam) did not have to overcome a very long distance to re-colonize meadows south of the dam and if we presume that many wild bees are at least similarly mobile as ground beetles (Wild bees perform various foraging flights per day, which can imply, mostly depending on body size, flights up to 600m; Gathmann & Tschardt, 2002; Greenleaf et al. 2007) it seems likely that highly mobile invertebrates like bees show similar resilience to flooding as ground beetle communities do. Fies et al. (2016), who collected butterflies on the same 32 sites (plus

additional 6 sites) as in this study, found exactly this pattern: immediately after the strong flood in 2013 butterfly numbers on meadows which had been inundated collapsed but within weeks, numbers of sightings per survey returned to normal levels. This implies that two consecutive years of but moderate flooding could have been enough time for substantial recovery of the bee community.

In support of this hypothesis, there was no significant difference in species numbers and proportions of soil nesting bees between northern and southern meadows. On the contrary, species accumulation curves even indicated southern meadows as more species-rich. As stated above, the proportion of shared species was only 36.8%, this could suggest a high discriminative power of inundation on the species composition of bee communities. But as the sub-communities on the different meadows underlie a high variation in general, the effect of flooding on species composition was significant, but rather weak. Even soil nesting bees, which have been assumed to be the species group strongest influenced by flooding, did not show any significant response to flooding concerning either the number of individuals, or proportions. These results can be taken as further evidence for high resilience of bee communities to flooding events.

Truxa and Fiedler (2012), who investigated moth communities in relation to flood regime across three riparian regions in lowland eastern Austria, found a relatively high proportion of stray species (ranging from 11% to 14%) in their dataset. In his well-known work about dynamics of regional distribution Hanski (1982) even went so far as to separate Bumblebee species in “core” and “satellite” species. Core species are widely distributed, which means they occupy most of the sites suitable for them, are locally abundant and are relatively well spaced out in the niche space whereas satellite species are uncommon and their abundance distribution is strongly influenced by local extinction and immigration dynamics. A more recent work about species abundance distributions of forest Hymenoptera by Ulrich and Ollik (2004) corroborates this distinction. Former studies have found highly skewed abundance distributions for wild bees (Potts et al., 2003; Tucker & Rehan, 2016), suggesting a high proportion of occasional, non-permanent species in the focal communities. As mentioned above, highly dynamic processes like extinction and recolonization play a big role in shaping the abundance distribution of such occasional species which in turn leads to a strong interdependence between local bee communities and the surrounding landscape matrix. With

regard on the regular disturbance regime south of the levee, one can assume a certain source to sink dynamic in the national park. In this case the wider non-flooded environment acting as source of new and recurring species and the regularly flooded areas acting as sink (Jones, 2011, Leibold et al., 2004). Even though bee species richness was predicted to be higher on southern meadows, I want to emphasize the particular importance of the wider surrounding (non-flooded) landscape which must play a crucial role in sustaining local bee diversity south of the dam.

Amarasekare and Nisbet (2001) proposed another noteworthy hypothesis in this context: They showed that a dispersal-competition trade-off can lead to local coexistence of superior and inferior competitors, provided the inferior competitor is superior at colonizing empty patches as well as immigrating among occupied patches. This means that less competitive bee species may thrive in areas where they would be usually excluded by other more competitive species because they have better colonization abilities. Regarding the high degree of disturbance through inundation and the associated local extinction and recolonization processes south of the dam (Gerisch et al., 2012; Fies et al., 2016), this dynamic surely plays an increased role in local community assembly processes in this region.

The Constrained Analysis of Principal Coordinates showed that flooding, total number of vascular plant species and floral abundance shaped species composition of wild bees. Still the model described only a small proportion of the whole variation, what implies that other factors must have a far stronger influence on bee species composition. Truxa and Fiedler (2012) concluded that despite regular flooding no characteristic forest moth community tolerant to inundation was apparent. In line with this, the number or proportion of bees which prefer cool and humid habitats was, contrary to expectation, not higher on southern meadows. Furthermore, Gerisch et al. (2012) found that assemblages of ground beetles inhabiting areas prone to flooding did not recover faster after a severe flooding event than those on rarely inundated plots. This could also be taken as evidence that local beetle communities in areas prone to flooding were not specifically adapted to regular inundation events. Altogether it seems like if the composition of insect communities does not adapt very well to the influence of regular flooding and therefore shows a low resistance to floods. Nevertheless rapid recolonization restores communities which are not especially flood resistant after a short while (Gerisch et al., 2012; Truxa & Fiedler, 2012; Fies et al., 2016).

However, although not significant, wild bees showed a 39% lower activity density south of the dam. As the estimated flower abundance was almost the same on both sides of the dam and because bees practice extensive maternal care which results in a relatively low reproduction rate (Strohm et al., 2002; Keasar, 2010), this effect may be an indication that the recovery of abundance is not yet completed. Since there are no records of bee abundances before the last big flooding event, it is currently impossible to test this hypothesis. Even so, the observed occurrence distribution of *Lasioglossum marginatum*, which are discussed in the next subchapter, may give a hint.

Although *Lasioglossum marginatum* was present on almost as many southern as northern meadows, individual numbers were extremely low and significantly smaller south of the levee. Due to its soil nesting habits, it might be reasonably assumed that most *L. marginatum* colonies south of the dam were wiped out during the last big flooding in 2013. *L. marginatum* colonies remain small during the first 4 to 5 years until the number of workers rises sharply in the 5th or 6th year when finally producing fertile males and females, following an almost exponential growth rate (Scheuchl & Willner, 2016). This means that colonies may have potentially existed even in the flood-prone areas, but had not yet grown to the same size as north of the levee. It would be extremely interesting to see how the numbers of *L. marginatum* will develop over the next 2 years.

Effects of mowing and vegetation traits

Even though meadows in the study area are supposed to be mown at least once a year on the grounds of conservation contracts, mowing in practice does not always occur regularly. Four of five meadows which had not been mown until the last sampling period in August 2016 were situated south of the levee. Three of these meadows had already been widely colonized by perennial herbs (such as *Arctium lappa*, *Solidago gigantea* or *Cirsium* sp.) and have gained characteristics of fallows, indicating that the last management interventions date back a couple of years. Steffan-Dewenter & Tschardt (2001) who studied wild bee communities on one- to five-year-old set-aside fields emphasized the high value of fallows which not only provide feeding sources but also suitable nesting habitats. Still, although some species groups may temporarily profit from abandonment, the characteristic vegetation and insect

communities of semi-natural, man-made grassland habitats on the long run depend on extensive mowing or grazing (Steffan-Dewenter & Leschke, 2003). Various papers about the influence of meadow management on wild bee communities agree that meadows with an intermediately intense management regime, with not more than two mowing events per year (as it was the case in the national park), provide appropriate habitats for diverse and stable bee communities (Weiner et al., 2011; Wastian et al., 2016). An extremely high influence of mowing cannot be denied: The mowing regime had a statistically significant effect on all parameters, defining activity densities or species numbers. This effect is logical, since mowing always led to an almost complete decline of potential feeding sources which certainly represents the most important attracting factor for wild bees (Holzschuh et al., 2007; Buri et al., 2014). Although a particularly severe negative effect on non-soil nesting bees could not be isolated, Holzschuh et al. (2010) showed that cavity-nesting bees are, compared to soil nesting bees, more often limited by a lack of nesting resources rather than by a lack of flower resources. Hence, non-soil nesting bees may benefit from temporary cessation of mowing as stems of perennial herbs represent an important nesting substrate for them (Scheuchl & Willner, 2016). However, a complete abandonment of management activities also won't be expedient as ultimately non-mown sites will develop into forest in the course of secondary succession (Falińska, 1998).

Network analyses

Network level

Results of the network analysis emphasize the high resilience of bee communities to flooding events: None of the examined network metrics were significantly different between annually flood prone and none flooded meadows. Mowing regime had also no significant influence on the observed metrics.

With 0.8 the mean $H2'$ of all meadows was very high compared with other studies (Popic et al., 2013; Carvalho et al., 2014; Zotarelli et al., 2014; Baldock et al., 2015) where values ranged between 0.4 and 0.6. This high value can either be an indication of extremely high specialization in the networks of this study or, more likely, of insufficient network data. Fründ

et al. (2015) stated that that a compilation of interaction data is prone to be incomplete even after intensive sampling. He further argued that this likely produces a sampling bias when regarding resource use specialization which generally results in an overestimation of specialization in a system. It seems likely that exactly this happened since many generalistic bee species were only observed on one or two different plants although they would have had the potential to feed on various other (e.g. less abundant) plant species.

Specialization (H2') was significantly higher in networks with fewer visited plant species. Since the proportion of polylectic bees did not show a detectable influence on this metric it is very likely that this effect was induced by the fact that there were some meadows which showed mass-occurrences of flowering plants during one or two sampling periods. This led to a high apparent specialization, or rather concentration, since most bees fed on the same highly abundant plant. This effect was probably mostly caused by vegetation traits and not by changes in bee species composition or foraging behavior (as described by Ebeling et al., 2011). Although in most cases the bees probably simply concentrated on the flowering plants which were most abundant, there were still some meadows which provided an exceptionally species poor range of flowering plants. As it involves a higher risk for a pollinator to rely on only one single plant species as a food source (Naeem & Li, 1997; Yachi & Loreau, 1999) it can be hypothesized that at least for some meadows the increased specialization was an indication for decreased stability of the system.

Larger vulnerability values indicate that plant species within a network are visited, or have their pollen transported by more diverse sets of animal species (Alarcón, 2010). It is therefore not surprising that the proportion of polylectic bees had a very strong influence on this metric, with a higher vulnerability in networks which comprise a higher proportion of polylectic bees. According to the insurance hypothesis, networks which are dominated by polylectic bee species are consequently potentially more stable (Naeem & Li, 1997; Yachi & Loreau, 1999) as it is more certain that if one pollinator drops out others will still provide pollination services. Although a little low, the mean vulnerability value was similar to those in former studies (Power & Stout, 2011; Popic et al., 2013). It can be hypothesized that this value would have been higher with more complete interaction data as a more exhaustive dataset would possibly reveal many interactions between already recorded bee and plant species which would in turn increase vulnerability values. Vulnerability also significantly decreased with increasing

individual-number of the honeybee *Apis mellifera*. Since this result was mainly caused by one single outlier value, it is questionable if the presence of honeybees had an actual effect on the vulnerability of the bee-flower networks in the study region. Since honeybees mostly occurred in large numbers when there was a mass flowering of a single plant species like *Solidago gigantea*, *Cirsium arvense* or *Salvia pratensis* and vulnerability is a weighted value, it seems possible that the algorithm over-weighted the value.

Overall, evidence is still mixed and controversial concerning the influence of domesticated bees on wild bees (Paini, 2004). Herbertsson et al. (2016) stated that competition between managed honeybees and wild bumblebees is highly dependent on landscape context. They found a displacement of bumblebees by honeybees in homogeneous landscapes, whereas in heterogeneous landscapes no such effect was detected. As the National Park Donau-Auen can be described as a heterogeneous landscape one would therefore expect that in this region the honey bee population does not have a significantly negative impact on wild bee communities. In line with this, in most analyses reported above the activity density of managed honeybees had no detectable effect on wild bee communities and their interaction networks with flowers.

Niche overlap in the observed networks ranged from 80 to 0.05 percent, the mean value of all meadows was 25%. This value corresponds with the high grade of specialization in the networks and is therefore a rather low value when compared to the findings of Power and Stout (2011) who found a value of 0.5 (50%) for organically managed and 0.4 (40%) for conventionally managed pastures. Following the aforementioned arguments about specialization, again this value would probably be higher with a more complete interaction dataset.

In networks with a smaller proportion of polylectic bees and more visited plant species niche overlap was significantly lower. These findings are expected since resource partitioning effects play an important role in shaping alimentary preferences (Ranta & Lundberg, 1980; Johnson, 1986; Blüthgen & Klein, 2011). Of course resource partitioning can only occur if there is at least a certain variety of resources (in this case flowering plant species) which can be partitioned among competing consumer species. Therefore, the large variation of this index is probably also influenced by mass flowerings on otherwise flower poor meadows which

resulted in a rather high actual niche overlap, because most bees then concentrated upon the mass-flowering plant species. The stability of insect–flower networks is thought to increase with a high degree of redundancy among its constituent species, because if a taxon is redundant in a network (has a similar interaction pattern to other species of the same trophic level) then its loss will not greatly destabilize the system (Power and Stout, 2011). Hence, generalist species again appear to stabilize the systems.

Since enhanced generalization in pollination networks tends to have a stabilizing effect on the systems properties the question arises what factors support the potentially unfavorable state of specialization and oligolecty. Praz et al. (2008) who tested how larvae of oligolectic bees develop when reared on non-host pollen went so far as to consider oligolecty of bees as an evolutionary constraint that has been repeatedly overcome by polylectic species, rather than an adaptive property favored under certain environmental conditions. They hypothesized that plants deliberately evolve adaptations to minimize pollen loss to pollen thieves or inefficient pollinators by narrowing down the spectrum of pollen-feeding visitors. Consequently bee specialization may be potentially beneficial for plants. Larsson (2005) found superior pollinator effectiveness of specialized pollinators as compared to generalized pollinators of the herb *Knautia arvensis* (*Caprifoliaceae*). He concluded that higher specialization of solitary bees could result in higher flower constancy and greater pollination success. Specialization can not only be quantified according to feeding habits of bees concerning taxonomic units of plants but also after feeding habits concerning individual traits, such as flower morphology, visual and olfactory signals, and temporal variation of feeding plants (Blüthgen & Klein, 2011). Exhaustive literature is available describing resource partitioning effects between *Bombus* species due to the length of their proboscis and the depth of blossom corollas (Ranta & Lundberg, 1980; Johnson, 1986). Heinrich (1976) even hypothesized that complete polylecty of bumblebees may lead to increased competition in bee communities which may ultimately decrease species richness. It follows that on the one hand increased specialization of bees is hypothesized to have a negative effect on the stability of an ecological network, but on the other hand it seems like plants are intentionally taking the risk of narrowing their range of potential pollinators to exclude non-efficient consumers and therefore optimize the cost–benefit ratio of involved pollination services.

Species level

All bee species with a particularly high network strength except of *Chelostoma florissomne* are highly generalistic and relatively common in the region. This is not at all surprising since the diversity of visited interaction partners has a strong influence on this index (Gilarranz et al., 2012). Although quantitatively calculated, the number of recorded individuals must have played a major role since the number of observed individuals per bee species correlated significantly with both, the diversity of plant species visited by each species and its actual species strength. Notably, in both aggregated networks the three bee species with the highest strength were social bees which was probably one of the main reasons for their higher numbers in the field (Scheuchl & Willner, 2016). The only oligolectic bee species with a high species strength was *Ch. florissomne* which is specialized on plant species in the Ranunculaceae family. Since *Ch. florissomne* was only found visiting flowers of 3 different plant species, but in high numbers, its species strength seems to be strongly influenced by the sheer number of records and the fact that plants of the Ranunculaceae family were barely visited by any other bee species.

On the meadows situated north of the levee the generalistic and widespread bumblebee species *Bombus pascuorum* had the by far highest species strength (9.81). This very high value (second strongest is *Lasioglossum marginatum* with a value of 3.4) was certainly resulting from its high abundance (64 observed individuals) and more important the, proportional to that, high number of visited plant species (32). Interestingly, even though *B. pascuorum* had a similar ratio of visited plant species compared to the number of observed individuals south of the dam (29 observed individuals interacting with 14 different plants), it had a way lower species strength (3.59) and fell behind *Lasioglossum calceatum* (11 observed individuals on 8 different plant species).

Whereas *Apis mellifica* showed an exceptionally high species strength south of the dam (7.12), it wasn't even under the top 10 strongest species in the northern area. More than twice as many honeybees were recorded south of the dam but most notably almost four times as many different plant species (North 3, South 11) were visited by honeybees south of the dam. Currently, there are only two beehives located in the national park, both of them north of the dam (C. Baumgartner, personal communication). Hence, the distribution of beehives in the

national park cannot explain the higher activity density on the southern meadows. Foraging ranges of honeybees can easily exceed distances of 5km and their ability to recruit fellow bees allows them to efficiently exploit sites which provide a high quantity of flowering plants even if these are several kilometers away from the hive (Couvillon et al., 20014; Couvillon et al., 2015). Since mean floral abundance was almost the same for both meadow categories it can be only speculated that the southern meadows simply provided more rewarding food resources for honeybees.

Conservation aspects and conclusion

Floodplains are highly dynamic systems which strongly underlie the processes of disturbance, local extinction and recolonization. These dynamics are strongly pronounced and play a major role in shaping the local plant and animal communities in the National Park Donau-Auen. The meadows in the regularly flooded part of the national park housed a more species-rich bee community than the meadows which are protected by the dam. However, bee communities south of the dam seem to be constantly threatened by local extinction through severe flooding events. Fortunately after such “tabula rasa” events recolonization seems to happen rather fast and a diverse bee community is restored by assembly from the regional meta-community after only a few years. To ensure such rapid recolonization it is most important that there are source areas from where bee species can re-distribute after flooding events. The non-flooded parts of the reserve are likely to act as an important source in that regard, but also from the surrounding landscape matrix recolonization events are likely to occur. Because of this strong link between flooded and non-flooded meadows it would not be useful to protect only the more diverse and dynamic meadows south of the dam. Rather, the northern meadows which are less dynamic but in return more stable over time have a clear conservation value in this respect. Another important aspect for conservation management is to maintain high beta diversity on the southern meadows which means to continue with the extensive management of the meadows but protect them from succession towards forest by mowing them at least occasionally every few years. Since mowing almost completely eliminates the food sources of bees at a short term, it is surely advisable to maintain the custom of unsynchronized mowing of the meadows as it also occurred during my sampling period.

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Appendix

Table 7. Catalogue showing species lists for each meadow and explaining which plant species were visited by each bee species.

	Individuals
N1	24
Andrena hattorfiana (FABRICIUS 1775)	3
Knautia arvensis	3
Andrena nitida (MÜLLER 1776)	1
Taraxacum officinale agg.	1
Apis mellifica	6
Knautia arvensis	5
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	7
Knautia arvensis	2
Lotus corniculatus	1
Vicia tenuifolia	4
Bombus rupestris (FABRICIUS 1793)	1
Knautia arvensis	1
Lasioglossum marginatum (BRULLÉ 1832)	4
Euphorbia cyparissias	2
Taraxacum officinale agg.	2
Lasioglossum nigripes (LEPELETIER 1841)	1
Knautia arvensis	1
Nomada armata (HERRICH-SCHÄFFER 1839)	1
Knautia arvensis	1
N10	16
Bombus sylvarum (LINNAEUS 1761)	1
Cerinth minor	1
Chelostoma florissomne (LINNAEUS 1758)	12
Ranunculus acris	2
Ranunculus polyanthemus	10
Eucera nigrescens (PÉREZ 1879)	1
Ajuga reptans	1
Lasioglossum marginatum (BRULLÉ 1832)	2
Ranunculus polyanthemus	2
N11	60
Andrena albobasiata (Thomson 1970)	1
Ornithogalum kochii	1
Andrena limata (SMITH 1853)	1
Pimpinella saxifraga	1
Andrena minutuloides (PERKINS 1914)	3
Pimpinella saxifraga	3
Andrena ovatula (KIRBY 1802)	1
Fragaria viridis	1
Apis mellifica	37
Salvia pratensis	37
Bombus haematurus (KRIECHBAUMER 1870)	2

Salvia pratensis	2
Bombus hortorum (LINNAEUS 1761)	1
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	1
Symphytum officinale	1
Bombus ruderarius (MÜLLER 1776)	1
Trifolium pratense	1
Bombus rupestris (FABRICIUS 1793)	1
Clinopodium vulgare	1
Bombus sylvarum (LINNAEUS 1761)	2
Clinopodium vulgare	1
Symphytum officinale	1
Bombus terrestris (LINNAEUS 1758)	1
Salvia pratensis	1
Chelostoma florissomne (LINNAEUS 1758)	2
Ranunculus polyanthemus	2
Halictus simplex/eurygnathus	1
Ranunculus polyanthemus	1
Lasioglossum marginatum (BRULLÉ 1832)	3
Ranunculus polyanthemus	3
Osmia adunca (PANZER 1798)	1
Leontodon hispidus	1
Osmia bicolor (SCHRANK 1781)	1
Fragaria viridis	1
N12	31
Andrena gravis (IMHOFF 1832)	1
Taraxacum officinale agg.	1
Andrena minutula (KIRBY 1802)	1
Taraxacum officinale agg.	1
Andrena nitida (MÜLLER 1776)	1
Taraxacum officinale agg.	1
Bombus pascuorum (SCOPOLI 1763)	2
Lathyrus pratensis	1
Taraxacum officinale agg.	1
Bombus terrestris (LINNAEUS 1758)	1
Taraxacum officinale agg.	1
Chelostoma distinctum (STÖCKHERT 1929)	2
Campanula patula	2
Chelostoma florissomne (LINNAEUS 1758)	5
Ranunculus polyanthemus	5
Heriades truncorum (LINNAEUS 1758)	1
Achillea millefolium agg.	1
Hylaeus cardioscapus (COCKERELL 1924)	1
Allium scorodoprasum	1
Hylaeus communis (NYLANDER 1852)	11
Allium scorodoprasum	11
Osmia cornuta (LATREILLE 1805)	1
Taraxacum officinale agg.	1
N13	43

Andrena gravida (IMHOFF 1832)	1
Taraxacum officinale agg.	1
Andrena hattorfiana (FABRICIUS 1775)	3
Knautia arvensis	3
Andrena limata (SMITH 1853)	1
Plantago media	1
Andrena taraxaci (GIRAUD 1861)	3
Taraxacum officinale agg.	3
Salvia pratensis	3
Bombus haematurus (KRIECHBAUMER 1870)	1
Salvia pratensis	1
Bombus humilis (ILLIGER 1806)	2
Lotus corniculatus	1
Salvia pratensis	1
Bombus hypnorum (LINNAEUS 1758)	1
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	9
Knautia arvensis	1
Lotus corniculatus	6
Plantago media	1
Trifolium repens	1
Bombus ruderalis (MÜLLER 1776)	1
Rhinanthus minor	1
Bombus terrestris (LINNAEUS 1758)	1
Pimpinella saxifraga	1
Bombus vestalis (GEOFFROY 1785)	1
Bunias orientalis	1
Chelostoma florisomne (LINNAEUS 1758)	2
Ranunculus polyanthemos	2
Colletes cunicularius (LINNAEUS 1761)	3
Euphorbia cyparissias	1
Taraxacum officinale agg.	2
Heriades truncorum (LINNAEUS 1758)	1
Leontodon hispidus	1
Lasioglossum calceatum (SCOPOLI 1763)	1
Plantago media	1
Lasioglossum laevigatum (Kirby 1802)	1
Bunias orientalis	1
Lasioglossum marginatum (BRULLÉ 1832)	2
Euphorbia cyparissias	1
Taraxacum officinale agg.	1
Lasioglossum nigripes (LEPELETIER 1841)	1
Knautia arvensis	1
Lasioglossum villosulum (KIRBY 1802)	3
Leontodon hispidus	3
Xylocopa violacea (LINNAEUS 1758)	1
Salvia pratensis	1
N14	14
Bombus pascuorum (SCOPOLI 1763)	2

Trifolium pratense	2
Chelostoma florissomne (LINNAEUS 1758)	9
Ranunculus polyanthemus	9
Heriades truncorum (LINNAEUS 1758)	1
Ranunculus polyanthemus	1
Lasioglossum calceatum (SCOPOLI 1763)	1
Ranunculus polyanthemus	1
Lasioglossum marginatum (BRULLÉ 1832)	1
Taraxacum officinale agg.	1
N15	50
Andrena albobasiata (Thomson 1970)	1
Ranunculus polyanthemus	1
Anthophora plumipes (PALLAS 1772)	1
Ajuga reptans	1
Apis mellifica	7
Knautia arvensis	3
Salvia pratensis	4
Bombus hortorum (LINNAEUS 1761)	2
Salvia pratensis	2
Bombus humilis (ILLIGER 1806)	2
Cirsium canum	1
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	8
Clinopodium vulgare	1
Prunella vulgaris	1
Salvia pratensis	3
Trifolium pratense	3
Chelostoma florissomne (LINNAEUS 1758)	20
Ranunculus polyanthemus	20
Lasioglossum calceatum (SCOPOLI 1763)	1
Cirsium canum	1
Lasioglossum malachurum (KIRBY 1802)	3
Agrimonia eupatoria	2
Cirsium canum	1
Lasioglossum villosulum (KIRBY 1802)	1
Leontodon hispidus	1
Lasioglossum zonulum (SMITH 1848)	2
Agrimonia eupatoria	1
Cirsium canum	1
Megachile ligniseca (KIRBY 1802)	1
Cirsium canum	1
Osmia leaiana (KIRBY 1802)	1
Cirsium canum	1
N16	60
Andrena albobasiata (Thomson 1970)	2
Trifolium pratense	2
Andrena minutula (KIRBY 1802)	1
Medicago lupulina	1
Apis mellifica	21

Salvia pratensis	19
Trifolium pratense	2
Bombus hortorum (LINNAEUS 1761)	3
Salvia pratensis	2
Trifolium repens	1
Bombus lapidarius (LINNAEUS 1758)	2
Trifolium pratense	2
Bombus lucorum (LINNAEUS 1761)	1
Trifolium pratense	1
Bombus pascuorum (SCOPOLI 1763)	6
Trifolium pratense	6
Chelostoma florissomne (LINNAEUS 1758)	10
Ranunculus polyanthemus	10
Eucera nigrescens PÉREZ 1879	1
Trifolium pratense	1
Halictus subauratus (ROSSI 1792)	1
Daucus carota	1
Halictus tumulorum (LINNAEUS 1758)	1
Trifolium pratense	1
Lasioglossum laevigatum (Kirby 1802)	1
Veronica chamaedrys	1
Lasioglossum marginatum (BRULLÉ 1832)	9
Ranunculus polyanthemus	2
Veronica chamaedrys	7
Lasioglossum pauxillum (SCHENCK 1853)	1
Salvia pratensis	1
N17	38
Andrena gelrae VAN DER VECHT 1927	1
Pimpinella saxifraga	1
Andrena gravis (IMHOFF 1832)	1
Ajuga genevensis	1
Anthophora plumipes (PALLAS 1772)	1
Ajuga genevensis	1
Apis mellifica	5
Salvia pratensis	5
Bombus hortorum (LINNAEUS 1761)	2
Salvia pratensis	2
Bombus pascuorum (SCOPOLI 1763)	5
Ajuga genevensis	3
Prunella vulgaris	1
Salvia pratensis	1
Chelostoma florissomne (LINNAEUS 1758)	12
Ranunculus polyanthemus	12
Eucera nigrescens (PÉREZ 1879)	1
Ajuga genevensis	1
Halictus rubicundus (CHRIST 1791)	1
Verbena officinalis	1
Lasioglossum laevigatum (Kirby 1802)	1
Veronica chamaedrys	1

Lasioglossum marginatum (BRULLÉ 1832)	6
Ranunculus polyanthemus	1
Veronica chamaedrys	5
Lasioglossum pauxillum (SCHENCK 1853)	1
Veronica chamaedrys	1
Osmia caerulea (LINNAEUS 1758)	1
Ajuga genevensis	1
N2	34
Andrena gravida (IMHOFF 1832)	1
Taraxacum officinale agg.	1
Andrena minutula (KIRBY 1802)	2
Leontodon hispidus	2
Andrena taraxaci (GIRAUD 1861)	1
Taraxacum officinale agg.	1
Bombus pascuorum (SCOPOLI 1763)	6
Lotus corniculatus	5
Trifolium pratense	1
Chelostoma florissomne (LINNAEUS 1758)	3
Leontodon hispidus	2
Ranunculus polyanthemus	1
Halictus sexcinctus (FABRICIUS 1775)	1
Leontodon hispidus	1
Halictus simplex/eurygnathus	2
Leontodon hispidus	2
Lasioglossum leucozonium (SCHRANK 1781)	1
Leontodon hispidus	1
Lasioglossum marginatum (BRULLÉ 1832)	12
Bellis perennis	1
Ranunculus acris	1
Taraxacum officinale agg.	10
Lasioglossum villosulum (KIRBY 1802)	2
Leontodon hispidus	2
Megachile octosignata (NYLANDER 1852)	1
Lotus corniculatus	1
Osmia caerulea (LINNAEUS 1758)	1
Leontodon hispidus	1
Osmia niveata (FABRICIUS 1804)	1
Leontodon hispidus	1
N3	11
Bombus hypnorum (LINNAEUS 1758)	1
Glechoma hederacea	1
Bombus pascuorum (SCOPOLI 1763)	3
Glechoma hederacea	3
Chelostoma distinctum (STÖCKHERT 1929)	1
Campanula patula	1
Chelostoma florissomne (LINNAEUS 1758)	5
Ranunculus polyanthemus	5
Lasioglossum marginatum (BRULLÉ 1832)	1
Taraxacum officinale agg.	1

N4	27
Andrena hattorfiana (FABRICIUS 1775)	1
Knautia arvensis	1
Andrena minutula (KIRBY 1802)	2
Erigeron annuus	1
Ranunculus polyanthemos	1
Apis mellifica	2
Knautia arvensis	1
Salvia pratensis	1
Bombus humilis (ILLIGER 1806)	1
Trifolium pratense	1
Bombus pascuorum (SCOPOLI 1763)	2
Cerinth minor	1
Trifolium pratense	1
Bombus rudericus (MÜLLER 1776)	1
Salvia pratensis	1
Bombus rupestris (FABRICIUS 1793)	1
Knautia arvensis	1
Bombus vestalis (GEOFFROY 1785)	6
Knautia arvensis	6
Chelostoma distinctum (STÖCKHERT 1929)	1
Campanula patula	1
Chelostoma florissomne (LINNAEUS 1758)	1
Ranunculus polyanthemos	1
Halictus subauratus (ROSSI 1792)	1
Centaurea jacea	1
Heriades truncorum (LINNAEUS 1758)	1
Erigeron annuus	1
Hylaeus communis (NYLANDER 1852)	1
Pimpinella major	1
Hylaeus gibbus (SAUNDERS 1850)	1
Erigeron annuus	1
Hylaeus sinuatus (SCHENCK 1853)	1
Pimpinella major	1
Lasioglossum leucozonium (SCHRANK 1781)	1
Knautia arvensis	1
Lasioglossum politum (SCHENCK 1853)	2
Erigeron annuus	1
Pimpinella major	1
Nomada armata (HERRICH-SCHÄFFER 1839)	1
Knautia arvensis	1
N5	18
Andrena hattorfiana (FABRICIUS 1775)	3
Knautia arvensis	3
Bombus hortorum (LINNAEUS 1761)	2
Salvia pratensis	1
Symphytum officinale	1
Bombus pascuorum (SCOPOLI 1763)	1
Vicia cracca	1

Bombus ruderarius (MÜLLER 1776)	1
Salvia pratensis	1
Chelostoma distinctum (STÖCKHERT 1929)	1
Campanula patula	1
Chelostoma florissomne (LINNAEUS 1758)	2
Ranunculus polyanthemus	2
Heriades truncorum (LINNAEUS 1758)	1
Ranunculus polyanthemus	1
N6	62
Andrena minutuloides (PERKINS 1914)	1
Daucus carota	1
Apis mellifica	22
Salvia pratensis	22
Bombus humilis (ILLIGER 1806)	12
Astragalus cicer	3
Centaurea jacea	1
Knautia arvensis	1
Lotus corniculatus	2
Scabiosa ochroleuca	1
Vicia tenuifolia	4
Bombus lapidarius (LINNAEUS 1758)	1
Lotus corniculatus	1
Bombus pascuorum (SCOPOLI 1763)	6
Astragalus cicer	2
Vicia tenuifolia	4
Bombus ruderarius (MÜLLER 1776)	1
Vicia tenuifolia	1
Bombus sylvarum (LINNAEUS 1761)	2
Scabiosa ochroleuca	1
Vicia tenuifolia	1
Bombus terrestris (LINNAEUS 1758)	1
Salvia pratensis	1
Chelostoma florissomne (LINNAEUS 1758)	7
Ranunculus polyanthemus	7
Halictus simplex/eurygnathus	1
Centaurea jacea	1
Halictus tumulorum (LINNAEUS 1758)	2
Dianthus pottederae	1
Euphorbia cyparissias	1
Lasioglossum majus (NYLANDER 1852)	1
Plantago media	1
Lasioglossum marginatum (BRULLÉ 1832)	2
Euphorbia cyparissias	1
Ranunculus polyanthemus	1
Lasioglossum pauxillum (SCHENCK 1853)	1
Ranunculus polyanthemus	1
Lasioglossum politum (SCHENCK 1853)	1
Daucus carota	1
Osmia caerulea (LINNAEUS 1758)	1

Salvia pratensis	1
N8	24
Andrena hattorfiana (FABRICIUS 1775)	1
Knautia arvensis	1
Bombus lapidarius (LINNAEUS 1758)	10
Astragalus cicer	1
Lotus corniculatus	2
Securigera varia	7
Bombus pascuorum (SCOPOLI 1763)	2
Lotus corniculatus	1
Securigera varia	1
Bombus terrestris (LINNAEUS 1758)	5
Securigera varia	5
Eucera longicornis (LINNAEUS 1758)	1
Vicia tenuifolia	1
Eucera nigrescens (PÉREZ 1879)	1
Vicia tenuifolia	1
Halictus quadricinctus (FABRICIUS 1776)	1
Knautia arvensis	1
Halictus tumulorum (LINNAEUS 1758)	2
Dianthus pottederae	2
Lasioglossum marginatum (BRULLÉ 1832)	1
Veronica chamaedrys	1
N9	19
Andrena ovatula (KIRBY 1802)	1
Valerianella locusta	1
Andrena saxonica (STÖCKHERT 1935)	1
Ornithogalum kochii	1
Apis mellifica	3
Salvia pratensis	3
Bombus haematurus (KRIECHBAUMER, 1870)	1
Salvia pratensis	1
Bombus hortorum (LINNAEUS 1761)	1
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	4
Medicago lupulina	1
Plantago lanceolata	1
Salvia pratensis	2
Bombus sylvarum (LINNAEUS 1761)	1
Lotus corniculatus	1
Chelostoma florissomne (LINNAEUS 1758)	3
Ranunculus polyanthemus	3
Halictus subauratus (ROSSI 1792)	1
Thlaspi perfoliatum	1
Lasioglossum laevigatum (Kirby 1802)	2
Euphorbia esula	1
Ornithogalum kochii	1
Xylocopa violacea (LINNAEUS 1758)	1
Salvia pratensis	1

S1	20
Bombus rupestris (FABRICIUS 1793)	1
Cirsium arvense	1
Bombus terrestris (LINNAEUS 1758)	2
Cirsium arvense	2
Eucera nigrescens PÉREZ 1879	1
Symphytum officinale	1
Halictus rubicundus (CHRIST 1791)	2
Cirsium arvense	2
Hylaeus communis NYLANDER 1852	6
Cirsium arvense	6
Hylaeus gibbus SAUNDERS 1850	1
Cirsium arvense	1
Lasioglossum clypeare (SCHENCK 1853)	1
Cirsium arvense	1
Megachile centuncularis (LINNAEUS 1758)	1
Cirsium arvense	1
Sphecodes albilabris (FABRICIUS 1793)	4
Cirsium arvense	4
Sphecodes pellucidus SMITH 1845	1
Cirsium arvense	1
S10	32
Anthophora crinipes SMITH 1854	1
Symphytum officinale	1
Apis mellifica	5
Symphytum officinale	5
Bombus barbutellus (KIRBY 1802)	1
Symphytum officinale	1
Bombus haematurus KRIECHBAUMER, 1870	2
Symphytum officinale	2
Bombus hortorum (LINNAEUS 1761)	2
Symphytum officinale	2
Bombus humilis ILLIGER 1806	1
Symphytum officinale	1
Bombus lucorum (LINNAEUS 1761)	3
Symphytum officinale	3
Bombus pascuorum (SCOPOLI 1763)	2
Symphytum officinale	2
Bombus ruderarius (MÜLLER 1776)	2
Symphytum officinale	2
Bombus sylvarum (LINNAEUS 1761)	1
Symphytum officinale	1
Bombus terrestris (LINNAEUS 1758)	7
Symphytum officinale	7
Hylaeus communis NYLANDER 1852	3
Allium scorodoprasum	1
Rorippa sylvestris	2
Hylaeus gibbus SAUNDERS 1850	1
Rorippa sylvestris	1

Lasioglossum calceatum (SCOPOLI 1763)	1
Allium scorodoprasum	1
S11	15
Andrena saxonica STÖCKHERT 1935	1
Ornithogalum kochii	1
Apis mellifica	2
Salvia pratensis	2
Bombus pascuorum (SCOPOLI 1763)	1
Salvia pratensis	1
Bombus sylvarum (LINNAEUS 1761)	2
Clinopodium vulgare	1
Prunella vulgaris	1
Chelostoma florissomne (LINNAEUS 1758)	6
Ranunculus polyanthemos	6
Heriades truncorum (LINNAEUS 1758)	2
Leontodon hispidus	2
Lasioglossum zonulum (SMITH 1848)	1
Leontodon hispidus	1
S12	79
Andrena chrysosceles (KIRBY 1802)	5
Euphorbia esula	5
Andrena nitida (MÜLLER 1776)	3
Euphorbia esula	3
Apis mellifica	46
Cirsium arvense	18
Euphorbia esula	28
Bombus haematurus KRIECHBAUMER, 1870	1
Cirsium arvense	1
Bombus lucorum (LINNAEUS 1761)	1
Allium scorodoprasum	1
Bombus pascuorum (SCOPOLI 1763)	3
Cirsium arvense	1
Prunella vulgaris	1
Verbena officinalis	1
Bombus terrestris (LINNAEUS 1758)	2
Allium scorodoprasum	1
Cirsium arvense	1
Chelostoma florissomne (LINNAEUS 1758)	2
Ranunculus polyanthemos	2
Colletes cunicularius (LINNAEUS 1761)	1
Euphorbia esula	1
Hylaeus communis NYLANDER 1852	4
Allium scorodoprasum	1
Cirsium arvense	2
Verbena officinalis	1
Hylaeus gibbus SAUNDERS 1850	2
Cirsium arvense	2
Lasioglossum laeve (KIRBY 1802)	1
Euphorbia esula	1

Lasioglossum laticeps (Schenck 1869)	1
Cirsium arvense	1
Lasioglossum leucozonium (SCHRANK 1781)	1
Ranunculus polyanthemos	1
Lasioglossum marginatum (BRULLÉ 1832)	1
Taraxacum officinale agg.	1
Lasioglossum pauxillum (SCHENCK 1853)	3
Calystegia sepium	2
Euphorbia esula	1
Lasioglossum zonulum (SMITH 1848)	1
Euphorbia esula	1
Nomada bifasciata OLIVIER 1811	1
Euphorbia esula	1
S14	74
Apis mellifica	44
Salvia pratensis	44
Bombus hortorum (LINNAEUS 1761)	3
Salvia pratensis	3
Bombus lapidarius (LINNAEUS 1758)	1
Lotus corniculatus	1
Bombus pascuorum (SCOPOLI 1763)	1
Salvia pratensis	1
Bombus sylvarum (LINNAEUS 1761)	1
Trifolium pratense	1
Chelostoma distinctum (STÖCKHERT 1929)	1
Campanula patula	1
Chelostoma florissomne (LINNAEUS 1758)	10
Ranunculus polyanthemos	10
Eucera nigrescens PÉREZ 1879	1
Trifolium pratense	1
Halictus subauratus (ROSSI 1792)	1
Achillea collina	1
Halictus tumulorum (LINNAEUS 1758)	2
Leucanthemum vulgare agg.	2
Lasioglossum calceatum (SCOPOLI 1763)	2
Centaurea jacea	1
Leontodon hispidus	1
Lasioglossum laticeps (Schenck 1869)	1
Leucanthemum vulgare agg.	1
Lasioglossum marginatum (BRULLÉ 1832)	1
Ranunculus polyanthemos	1
Panurgus calcaratus (SCOPOLI 1763)	3
Leontodon hispidus	3
Sphecodes albilabris (FABRICIUS 1793)	1
Leontodon hispidus	1
Xylocopa valga GERSTAECKER 1872	1
Salvia pratensis	1
S15	30
Andrena gravida IMHOFF 1832	1

Trifolium pratense	1
Andrena simontornyella NOSKIEWICZ 1939	1
Veronica chamaedrys	1
Apis mellifica	10
Securigera varia	5
Trifolium pratense	5
Bombus hortorum (LINNAEUS 1761)	1
Trifolium pratense	1
Bombus pascuorum (SCOPOLI 1763)	4
Trifolium pratense	4
Chelostoma florisomne (LINNAEUS 1758)	4
Ranunculus acris	2
Ranunculus polyanthemus	2
Eucera nigrescens PÉREZ 1879	3
Trifolium pratense	2
Vicia angustifolia	1
Halictus subauratus (ROSSI 1792)	1
Trifolium pratense	1
Halictus tumulorum (LINNAEUS 1758)	3
Tragopogon orientalis	1
Trifolium pratense	2
Lasioglossum marginatum (BRULLÉ 1832)	1
Veronica chamaedrys	1
Lasioglossum zonulum (SMITH 1848)	1
Ranunculus acris	1
S16	114
Apis mellifica	101
Solidago gigantea	101
Bombus terrestris (LINNAEUS 1758)	1
Solidago gigantea	1
Ceratina cyanea (KIRBY 1802)	2
Centaurium erythraea	1
Erigeron annuus	1
Coelioxys inermis (KIRBY 1802)	1
Solidago gigantea	1
Halictus rubicundus (CHRIST 1791)	1
Solidago gigantea	1
Halictus subauratus (ROSSI 1792)	1
Erigeron annuus	1
Heriades truncorum (LINNAEUS 1758)	2
Erigeron annuus	1
Solidago gigantea	1
Hylaeus communis NYLANDER 1852	1
Solidago gigantea	1
Hylaeus intermedius FÖRSTER 1871	1
Solidago gigantea	1
Hylaeus rinki (GORSKI 1852)	1
Agrimonia eupatoria	1
Lasioglossum zonulum (SMITH 1848)	1

Centaurium erythraea	1
Sphecodes albilabris (FABRICIUS 1793)	1
Solidago gigantea	1
S17	34
Andrena ovatula (KIRBY 1802)	1
Veronica chamaedrys	1
Andrena pallitarsis PÉREZ 1903	5
Pimpinella major	5
Apis mellifica	10
Glechoma hederacea	1
Salvia pratensis	9
Bombus humilis ILLIGER 1806	1
Trifolium pratense	1
Chelostoma florissomne (LINNAEUS 1758)	1
Ranunculus polyanthemus	1
Eucera longicornis (LINNAEUS 1758)	1
Vicia tenuifolia	1
Eucera nigrescens PÉREZ 1879	1
Vicia angustifolia	1
Halictus subauratus (ROSSI 1792)	1
Achillea millefolium agg.	1
Halictus tumulorum (LINNAEUS 1758)	2
Trifolium pratense	1
Verbena officinalis	1
Hylaeus intermedius FÖRSTER 1871	2
Pimpinella major	2
Lasioglossum laevigatum (Kirby 1802)	2
Ornithogalum kochii	1
Ranunculus polyanthemus	1
Lasioglossum marginatum (BRULLÉ 1832)	2
Veronica chamaedrys	2
Lasioglossum paucillum (SCHENCK 1853)	3
Leucanthemum vulgare agg.	3
Lasioglossum politum (SCHENCK 1853)	1
Pimpinella major	1
Lasioglossum zonulum (SMITH 1848)	1
Verbena officinalis	1
S2	9
Apis mellifica	1
Salvia pratensis	1
Bombus hortorum (LINNAEUS 1761)	1
Salvia pratensis	1
Bombus humilis ILLIGER 1806	1
Salvia pratensis	1
Chelostoma florissomne (LINNAEUS 1758)	4
Ranunculus polyanthemus	4
Heriades truncorum (LINNAEUS 1758)	2
Erigeron annuus	2
S3	24

Andrena albobasiata (THOMSON 1970)	1
Trifolium pratense	1
Andrena bisulcata (MORAWITZ 1877)	1
Daucus carota	1
Andrena fulvicornis (SCHENCK 1853)	2
Daucus carota	2
Andrena minutuloides (PERKINS 1914)	4
Daucus carota	4
Apis mellifica	9
Centauera stoebe	8
Salvia pratensis	1
Bombus humilis (ILLIGER 1806)	3
Centauera stoebe	1
Lotus corniculatus	1
Trifolium pratense	1
Chelostoma florisomne (LINNAEUS 1758)	2
Ranunculus polyanthemos	2
Hylaeus communis (NYLANDER 1852)	1
Daucus carota	1
Hylaeus pictipes (NYLANDER 1852)	1
Daucus carota	1
S4	7
Andrena hattorfiana (FABRICIUS 1775)	1
Knautia arvensis	1
Apis mellifica	2
Knautia arvensis	2
Bombus argillaceus (SCOPOLI 1763)	1
Knautia arvensis	1
Heriades truncorum (LINNAEUS 1758)	1
Achillea millefolium agg.	1
Lasioglossum discum (SMITH 1853)	1
Knautia arvensis	1
Lasioglossum marginatum (BRULLÉ 1832)	1
Ranunculus polyanthemos	1
S5	14
Bombus haematurus (KRIECHBAUMER, 1870)	1
Symphytum officinale	1
Bombus hortorum (LINNAEUS 1761)	2
Symphytum officinale	2
Bombus pascuorum (SCOPOLI 1763)	6
Symphytum officinale	6
Bombus rupestris (FABRICIUS 1793)	1
Symphytum officinale	1
Bombus terrestris (LINNAEUS 1758)	1
Symphytum officinale	1
Chelostoma florisomne (LINNAEUS 1758)	2
Ranunculus polyanthemos	2
Eucera nigrescens (PÉREZ 1879)	1
Lathyrus pratensis	1

S6	65
Andrena albobasiata (Thomson 1970)	1
Solidago gigantea	1
Andrena flavipes (PANZER 1799)	1
Solidago gigantea	1
Andrena limata (SMITH 1853)	1
Solidago gigantea	1
Anthophora furcata (PANZER 1798)	1
Stachys palustris	1
Apis mellifica	42
Arctium lappa	9
Glechoma hederacea	2
Solidago gigantea	31
Bombus haematurus (KRIECHBAUMER, 1870)	1
Symphytum officinale	1
Bombus hortorum (LINNAEUS 1761)	1
Symphytum officinale	1
Bombus humilis (ILLIGER 1806)	1
Vicia cracca	1
Bombus pascuorum (SCOPOLI 1763)	2
Symphytum officinale	1
Vicia cracca	1
Heriades truncorum (LINNAEUS 1758)	3
Solidago gigantea	3
Hylaeus communis (NYLANDER 1852)	8
Solidago gigantea	8
Lithurgus cornutus (FABRICIUS 1787)	1
Arctium lappa	1
Megachile centuncularis (LINNAEUS 1758)	1
Arctium lappa	1
Xylocopa violacea (LINNAEUS 1758)	1
Arctium lappa	1
S7	15
Bombus pascuorum (SCOPOLI 1763)	8
Lathyrus pratensis	3
Symphytum officinale	5
Chelostoma florissomne (LINNAEUS 1758)	2
Ranunculus polyanthemus	2
Eucera nigrescens (PÉREZ 1879)	2
Symphytum officinale	2
Lasioglossum calceatum (SCOPOLI 1763)	1
Barbarea vulgaris	1
Lasioglossum marginatum (BRULLÉ 1832)	1
Barbarea vulgaris	1
Lasioglossum zonulum (SMITH 1848)	1
Lythrum salicaria	1
S8	24
Andrena humilis (IMHOFF 1832)	3
Tragopogon orientalis	3

Apis mellifica	2
Salvia pratensis	2
Bombus hortorum (LINNAEUS 1761)	1
Salvia pratensis	1
Bombus pascuorum (SCOPOLI 1763)	1
Salvia pratensis	1
Chelostoma florisomne (LINNAEUS 1758)	1
Ranunculus polyanthemus	1
Colletes hylaeiformis (EVERSMANN 1852)	1
Achillea millefolium agg.	1
Halictus quadricinctus (FABRICIUS 1776)	2
Tragopogon orientalis	2
Halictus subauratus (ROSSI 1792)	4
Achillea millefolium agg.	4
Lasioglossum albipes (FABRICIUS 1781)	1
Tragopogon orientalis	1
Lasioglossum buccale (PÉREZ 1903)	1
Taraxacum officinale agg.	1
Lasioglossum calceatum (SCOPOLI 1763)	6
Achillea millefolium agg.	3
Plantago lanceolata	1
Tragopogon orientalis	2
Lasioglossum leucozonium (SCHRANK 1781)	1
Tragopogon orientalis	1
S9	17
Andrena gravida (IMHOFF 1832)	1
Tragopogon orientalis	1
Andrena taraxaci (GIRAUD 1861)	5
Taraxacum officinale agg.	5
Apis mellifica	1
Salvia pratensis	1
Bombus lucorum (LINNAEUS 1761)	1
Trifolium pratense	1
Bombus pascuorum (SCOPOLI 1763)	1
Trifolium pratense	1
Lasioglossum calceatum (SCOPOLI 1763)	1
Ornithogalum kochii	1
Lasioglossum marginatum (BRULLÉ 1832)	3
Euphorbia esula	2
Taraxacum officinale agg.	1
Lasioglossum nigripes (LEPELETIER 1841)	3
Tragopogon orientalis	3
Lasioglossum xanthopus (KIRBY 1802)	1
Tragopogon orientalis	1

Abstract

It is widely known that intensity and predictability of inundation events may have a strong influence on the species composition of plant communities, which in turn shapes the species composition of the associated fauna. Extreme population declines of insect species caused by floods have often been described in the literature. Yet, not much is known about the long term effects of such severe events, especially at the level of entire communities or their biotic interactions. In this study bee communities on meadows which are almost annually flooded by the Danube River were compared with communities on meadows which are rarely subject to inundation events. Flower-visiting bees were sampled on 32 meadows in the National Park Donau-Auen four times between late April and early August 2016. Sixteen of the selected meadows were situated on the flood-prone and another 16 on the protected side of a levee which stretches through the reserve. Altogether, I recorded 92 wild bee species interacting with flowers of 62 plant species. Mowing activities and strongly related to that, abundance of feeding plants were the main drivers altering wild bee activity density and diversity. Counter to expectations, the flooding regime had no significant impact on observed individual numbers and species accumulation curves suggest that the species richness was higher on meadows which are more regularly flooded. As a potential driver of this pattern, a significantly higher bee differentiation diversity on annually flooded meadows could be identified. Since bees are predicted to be highly vulnerable to floods, it follows that bee assemblages must have recovered following the last unusually severe summer flood in 2013. To obtain further insight into the functional characteristics of the observed bee communities in relation to pollination, three network metrics, which were derived from a bipartite plant-bee interaction matrix, were analyzed. None of the network indices was affected by the flooding regime. Hence it is concluded that, although floods may have a devastating effect on wild bee populations in the short term, recolonization happens rather quickly, restoring stable and diverse bee communities only after a few years. These findings reinforce earlier studies in which other insect groups seemed to show a low resistance but high resilience towards flooding. The observed resilience surely highly depends on the surrounding landscape, which acts as a starting point for recolonization processes. Hence it is extraordinary important for this area to consider biodiversity not only locally but on a wider, landscape comprising scale.

Zusammenfassung

Viele Studien beschrieben einen starken Einfluss von regelmäßige Überflutungen auf lokale Pflanzengemeinschaften. Weniger bekannt ist inwiefern sich Überschwemmungen auf die lokale Fauna auswirken. Für viele Insektengruppen wurden bereits extreme Populationsrückgänge nach Überflutungen beschrieben. Wie sich die Artengemeinschaften nach solch einem einschneidendem Ereignis langfristig entwickeln bleibt allerdings meist offen. In dieser Studie vergleiche ich Wildbienen-Gemeinschaften auf Wiesen die beinahe jährlich überschwemmt werden, mit solchen die nur sehr selten einer derartigen Störung ausgesetzt sind. Ein optimales Umfeld für solch eine Untersuchung bietet der Nationalpark Donau-Auen welcher durch den Marchfeld-Schutzdamm in zwei klare Bereiche gegliedert werden kann: Die Nördliche Hälfte des Parks wird durch den Damm beinahe vollkommen vor Überschwemmungen bewahrt, während bei höheren Pegelständen der Donau die südliche Hälfte regelmäßig geflutet wird. Insgesamt wurden 32 Wiesen an 4 verschiedenen Terminen in der Zeit von Ende April bis Anfang August 2016 besammelt. Während dieser Zeit wurden 1103 Individuen und 93 Bienen Arten aufgezeichnet. Zweifelsohne hatte die Mahd der Wiesen und der damit verbundene starke Rückgang an potentiellen Futterpflanzen den größten Einfluss auf die Aktivität und Diversität der Wildbienen. Entgegen aller Erwartungen hatte der Hochwassereinfluss keinen signifikant negativen Effekt auf die Wildbienen-Aktivitätsdichte und individuenbezogene als auch standortbezogene Akkumulationskurven suggerierten sogar einen höheren Artenreichtum auf regelmäßig gefluteten Wiesen. Als potenzielle Erklärung dafür konnte eine heterogenere Fauna auf den südlichen Wiesen festgestellt werden. Da Wildbienen in früheren Arbeiten als sehr empfindlich gegenüber Überschwemmungen eingestuft wurden, müssen sich die Wildbienen-Gemeinschaften seit dem extrem starken Hochwasser im Jahr 2013 weitgehend erholt haben. Folglich darf von einer hohen Elastizität gegenüber diesem Umwelteinfluss ausgegangen werden. Um einen tieferen Einblick in die funktionellen Charakteristika der beobachteten Wildbienen-Communitys zu erlangen wurde zusätzlich ein Pflanzen-Bestäuber Netzwerk erstellt und daraus drei verschiedene Netzwerk-Metriken berechnet. Der Hochwassereinfluss hatte auf keinen der drei untersuchten Werte einen Einfluss. Folglich scheint es als ob, obwohl Wildbienen sehr sensibel auf Überschwemmungen reagieren, in den betroffenen Regionen eine rasche Erholung der Individuen und Artenzahlen einsetzt. Eine solche erscheint allerdings

nur dann möglich, wenn die weitere Umgebung als Ausgangsort für Rekolonisationprozesse dienen kann. In Anbetracht dessen ist es besonders in dieser Region von hoher Bedeutsamkeit Biodiversität auf einer größeren landschaftlichen Ebene zu betrachten.