

## Original Articles

# Are bees attracted by flower richness? Implications for ecosystem service-based policy

J. Liira <sup>a,\*</sup>, I. Jürjendal <sup>b</sup>

<sup>a</sup> Institute of Ecology and Earth Science, University of Tartu, Estonia

<sup>b</sup> Tallinn Botanic Garden, Tallinn, Estonia

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## ABSTRACT

Agri-environmental policies aim to reverse the degradation of ecosystem services in rural landscapes by implementing biodiversity-based land-use solutions. One such agri-environmental measure is the contract for bee-forage fields in Estonia. We developed a multi-site experiment to estimate the effect of plant diversity on the quality properties of flower-based services, such as flowering duration (indicating functional stability) and the foraging activity of insect pollinators (indicating functional intensity). Each site consisted of eight randomly ordered strip-segments forming a flower diversity gradient.

The period of abundant flowering was longer in all kinds of species mixture than in monocultures. However, the foraging activity of honey bees and bumblebees was greatest in monocultures and in a low-diversity mixture, while a balanced high-diversity mixture was least attractive. Foraging activity was lowered when an abundant melliferous plant species was flowering within a high-diversity mixture (i.e. high species richness, but low evenness). The extended flowering of species mixtures did not compensate for the lower daily visitation rate.

We challenge the largely biodiversity-oriented agricultural policy designs. This case study provides evidence that plant species richness is not a comprehensive indicator of the service provision quality of an ecosystem. Specifically, low-diversity flower areas are the best foraging sites for bees and other flower visitors. A field mosaic of various monocultures and low-diversity mixtures seems to be the ecologically most efficient rural landscape design to support bees and other potential pollinators. Suggested and marketed pollinator-oriented seed mixtures should be quantitatively tested for ecological efficiency.

## 1. Introduction

Ecosystem services in rural landscapes ensure quality of life in human societies (Costanza et al., 1997), but their long term sustainability is threatened by the degradation of ecological networks (Billeter et al., 2008; Cardinale et al., 2012; Emmerson et al., 2016). Pollinator declines have received particular attention among the public and in policy developments (Potts et al., 2010; Hall and Martins, 2020). The replacement of traditional natural forage habitats with short-rotation crop areas is considered the most visible cause of pollinator declines (Biesmeijer et al., 2006; Scheper et al., 2014; Jones et al., 2021). European agri-environmental policy aims to reduce land use damage by implementing nature-oriented solutions (Dicks et al., 2014; Pe'er et al., 2014; Geijzendorffer et al., 2017), including measures to recover the forage basis for pollinators, such as flower-rich field margins or fields of melliferous flower crops (also called bee-crops) (Haaland et al., 2011;

Buhk et al., 2018; Kolkman et al., 2022). In Estonia, the earlier agri-environmental measures program (2015–2022) and the present eco-schemes program (since 2023) include an optional contract for farmers to establish flower-crop fields for honey bees (Runge et al., 2022). This contract obliges farmers to cultivate at least three different flower species as monocultures or as a mixture, which should form a continuously flowering forage conveyer during an extended season (Runge et al., 2022). The primary (official) aim of these flower fields is to improve the forage basis for honey bees, with the expectation that this increases the production of honey and bee bread (i.e., provisional service of flowers mediated by honey bees), and improves the maintenance forage basis for bee colony health in flower poor seasons. A secondary aim of the contract reflects the expectation that many wild pollinators also benefit from these flower rich areas as a supplementary forage basis (Evans et al., 2018). The enhanced forage basis of honey bees, wild bees and other insect pollinators is expected to result in improved regulative

\* Corresponding author.

E-mail address: [jaan.liira@ut.ee](mailto:jaan.liira@ut.ee) (J. Liira).

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services, such as the pollination of crops (Garibaldi et al., 2013; Bartomeus et al., 2014; Kleijn et al., 2015) and native plant species (Porto et al., 2020; Su et al., 2022). However, the degree to which monocultures and flower mixtures with different diversity levels provide efficient forage sources has not been precisely estimated, meaning that cost-efficient design of flower areas is still under development. Here, we provide an empirical test of the effect of flower diversity on forage provision quality for various insect pollinators.

As with any other ecosystem service, flower service has three main properties defining its quality: functional diversity, functional stability and functional intensity (Kütt et al., 2018) (also summarised in Fig. S1). In ecological theory and the design of environmental policy, biodiversity is considered one of the best target indicators (Balvanera et al., 2006; Isbell et al., 2011; Herzon et al., 2018; Elmiger et al., 2023) because it associates well with the stability of ecosystem service provision (service duration and resilience to disturbance), which itself is explained via increased functional diversity of service providers (Tilman and Downing, 1994; Tilman et al., 1997; Yachi and Loreau, 1999; Isbell et al., 2011). However, beyond functional stability and functional diversity, the functional intensity of a service is also an important feature. Simple examples of functional intensity include biomass productivity, plant height, flower functional size and leaf photosynthetic activity, but also the aesthetic value of a community. The relationship between biodiversity and the functional intensity of an ecosystem is generally expected to be positive, either linear or curved, with saturation at a medium level of diversity (Loreau et al., 2001; Cardinale et al., 2011), but the trend can theoretically also be concave (Paul et al., 2020). The non-linear form may be explained by the misleading scale extension generated by biodiversity indicators (e.g. species richness), which over-emphasizes the role of rare or subordinate species in the community (Diaz and Cabido, 2001; Kütt et al., 2016), while most of the service is provided by a small subset of (co-)dominant species. This is called functional redundancy among species (Carreck and Williams, 1997; de Bello et al., 2012; Liira et al., 2019). Discussion about the type and shape of the relationship between biodiversity and the service provision intensity is ongoing, because there is a deficit of true quantitative case studies and experiments (Kremen et al., 2007; Kleijn et al., 2015). Here, we provide empirical data to help fill this knowledge gap.

Species-rich habitats and ornamental flower mixtures are aesthetically valued (Junge et al., 2009; Sidhu and Joshi, 2016; Hoyle et al., 2018), but the human perspective can be a biased indicator of pollinator perception (Wood et al., 2015; Kütt et al., 2016; Kütt et al., 2018). There exists ambivalence among beekeepers and farmers about the functional value of these flower areas, the species and mixtures used, and certain management aspects (Mante and Gerowitt, 2007; Breeze et al., 2019). Pollinator-oriented, species-rich flower seed mixtures are also costly (relative to the cost of common flower crops), and mixed flower areas can be complicated to maintain (Otto et al., 2017; Scheper et al., 2021). Even bee-oriented flower mixtures do not always account for the behavioural peculiarities of social pollinators (Carreck and Williams, 1997, 2002; Alanen et al., 2011; Rundlöf et al., 2014) and may not be sufficiently seasonally adjusted (Carreck and Williams, 1997; Ebeling et al., 2008; von Königslöw et al., 2022). The foraging activity of various pollinator groups is known to be dependent on the abundance of flowers, and the shape of the relationship is taxon specific (Sih and Baltus, 1987; Ebeling et al., 2008; Jha and Vandermeer, 2009). For example, while social pollinators tend to focus on some resource rich flower patches (Hegland and Totland, 2005; Venjakob et al., 2016; Marja et al., 2018), wild solitary pollinators usually disperse between different sources (Sih and Baltus, 1987; Ebeling et al., 2008; Jha and Vandermeer, 2009). A diversity of simultaneously flowering plant species at a site can create a distraction for flower-visiting foragers (Kunin 1993; Otto et al., 2017; Albor et al., 2019). In many studies of flower areas, analyses have also struggled to differentiate between the effect of plant species diversity, effects of flower abundance, and confounding environmental conditions (Hegland and Boeke, 2006; Ebeling et al., 2008). Therefore, objective

experimental evidence about the functional efficiency of bee-crop areas and of flower mixtures is still required.

Our objective was to quantify the effect of biodiversity on the provision quality of an ecosystem service, and specifically on the functional stability and functional intensity of the service. We designed a multi-site field experiment where we estimated the flowering duration and foraging activity of insect pollinators along a diversity gradient of melliferous plants (bee-crops). We assumed that the number of weeks with abundant flowering is a robust indicator of service provision stability, and the number of flower-visiting insects is a robust indicator of the flower service intensity. At each site, flowering strips of similar size represented different levels of diversity and simultaneously competed for the attention of insect pollinators, reducing the effect of confounding contextual factors (e.g. landscape structure). We tested the working hypothesis (Hypothesis 1) that the flowering duration and foraging activity of insect pollinators both have a positive saturation-type relationship in response to increasing plant species diversity, as predicted by the theory of functional redundancy and emphasizing that the service provision is driven by the subset of species. To more sensitively quantify the shape of the relationship and assess the role of functional redundancy (i.e. the leading role of dominant service providers), we additionally tested another working hypothesis. Hypothesis 2 stated that if the main service provider effect prevails then the functional response of the flower community with an abundant species and many subordinate species (i.e. high species richness but low diversity) should not differ from the service level provided by a monoculture. An alternative outcome within this hypothesis would be that the diversity of neighbouring plant species complements the functionality of the dominant species and the service quality of this community is similar to the level observed in a high-diversity flower mixture (high species richness, diversity and evenness). We tested both hypotheses using two levels of analysis: (i) with a theoretical focus on the effect of diversity and (ii) with an applied focus on particular treatments to promote knowledge among end-users. When estimating functional intensity, we separately addressed three groups of flower visiting insects (potential pollinators): honey bees, bumblebees and other conspicuous insect pollinators (i.e. solitary bees, syrphids and butterflies in combined), because the shape of the activity-diversity relationship may differ between these groups as a result of their social and synecological behaviour.

## 2. Material and methods

### 2.1. Experimental design

Experimental sites were mostly distributed over an area of approximately 75 × 75 km in south-eastern Estonia; a smaller number of sites were located further to the north and west (maps Fig. S2). We carried out two rounds of single-season experiments, in 2021 and 2022. When positioning experimental sites in the landscape, we considered the criteria used in the Estonian agri-environmental contract for bee forage-crop areas (legislative information for the period 2014 – 2020 <https://www.riigiteataja.ee/akt/106102022003>; and for the period 2023 – 2027 <https://www.riigiteataja.ee/akt/118042023011>). Accordingly, most sites were positioned in agricultural landscapes, near groups of honey bee hives. We used the margins of spring-sown crop fields, ploughed or otherwise prepared for the crop. Sites were positioned at a distance between tens and several hundred meters from the nearest group of hives, as the contract criteria prescribe. Group size varied, and sometimes there were fewer than the prescribed minimum of ten hives, but the minimum (two – three hives) was more than sufficient for the purposes of the experiment. It was also expected that hive locations indicate suitable forage landscapes for natural pollinators, as beekeepers typically search carefully for the best flower-rich landscapes (Evans et al., 2018). The role of honey bees as potential suppressors of native pollinators is still under discussion (Butz Huryn 1997; Paini 2004; Mallinger et al., 2017), and it is notable that neutral or positive



correlations between honey bees and wild pollinator abundances can also be found (Garibaldi et al., 2013; Evans et al., 2018). Maps of crop fields and hive groups were obtained from the Agricultural Registers and Information Board of Estonia (Map server <https://kls.pria.ee/kaart>), and the early-season status of fields was assessed using Copernicus Sentinel-2 satellite images provided by the Estonian Land Board 'Satiladu' service (<https://satiladu.maaamet.ee>). In total, 42 experimental sites were initiated, but only 33 of them reached an acceptable stage for the survey of pollinator foraging activity (18 sites in 2021 and 15 sites in 2022). Most individual sites were used only in a single year because of the crop rotation in these fields. A few test sites were initiated in the botanical gardens of Tartu and Tallinn for the additional purpose of public dissemination.

Using field maps publicly available at the Agricultural Registers and Information Board of Estonia (Map server <https://kls.pria.ee/kaart>) and topographic land cover maps from the Estonian Land Board (<https://maaamet.ee>), we estimated land use within a 3 km radius of each site (the average foraging range of honey bees) (Beekman and Ratnieks, 2000; Steffan-Dewenter and Kuhn, 2003). An average experimental site was surrounded by 35% of forest, woodland or shrub land, 33% of agricultural land and 18% of garden, yard or other anthropogenic habitat (see Table 1 for details). Various types of wetland were rare (1.3%), and semi-natural (potentially flower rich) grasslands were small and scattered. In the year of the experiment at each site, summer-flowering crops of potential interest to pollinators covered on average 4% of the landscape. Most commonly, these summer-crops were conventionally-managed fields with spring oil seed rape or rapeseed and field mustard (*Brassica napus* and *Brassica rapa*), buckwheat (*Fagopyrum esculentum*) and field bean (*Vicia faba*), or green fallow areas with *Trifolium* sp. and *Medicago* sp.. During visits to sites, we observed that the main mass-flowering honey bee forage plants in surrounding natural habitats were *Aegopodium podagraria*, *Athriscus sylvestris*, *Epilobium angustifolium*, *Filipendula ulmaria* and *Rubus idaeus*. Among woody vegetation, *Tilia* species, hybrids and varieties growing in ornamental areas were the main competing attractors.

We developed an original experimental design that allowed pollinators to choose between different diversity treatments at individual sites, thus minimizing site-specific effects of landscape composition, soil conditions and weather. At each site, we created a diversity gradient using eight treatments. Seeds were sown in excess into consecutive 10 cm wide × 10 m long strip sections in a random order, leaving one-meter breaks between treatments, producing a ca 90 m experimental strip (Fig. S3). The long and narrow strip design makes the detection and counting of flower visitors very time efficient. We tested such a design in previous years and found it to be effective for attracting honey bees, bumblebees and other pollinators (unpublished trials from two previous years with various species and seed mixtures).

The treatments consisted of three different monocultures, one low-diversity mixture of the same three species, and four different high-diversity mixtures. Among the high-diversity treatments, one treatment consisted of a high-diversity mixture with balanced species proportions – this was the treatment with highest diversity (high species number and high evenness). The other three high-diversity treatments had one forage species as a (co-)dominant (the same species used in monoculture), meaning high species number but with lower evenness of

species. This was needed to precisely test the effect of diversity on foraging activity in the high species richness conditions. We used borage (*Borago officinalis*), cornflower (*Centaurea cyanus*) and lacy phacelia (*Phacelia tanacetifolia*) in the monoculture treatments; their mixture as the low-diversity mixture treatment; and all three as dominants in the high-diversity mixture varieties. The treatments of high-diversity mixtures with a dominant were completed by combining each dominant with a balanced high-diversity seed mixture. The balanced high-diversity seed mixture contained a combination of several commercially available pollinator-oriented annual flower mixtures. Species-rich seed mixtures were selected based on the product information indicating that the mixture had a specific quality to attract bees and consisted only of flower species (mixtures with grasses were not used). Some of the commercial mixtures were described as consisting of 'wild plant species'; however, the component species listed on the package or the species that emerged in the field did not necessarily support this: most were common ornamental species from European gardens or cultivated varieties of native species (e.g. cornflower varieties of various colour or sometimes with double-blossoms). All seeds for monocultures and mixtures were obtained from various European seed companies and then combined before sowing to homogenise the genetic diversity within species and to reduce differences between suppliers in the choice of species and varieties in mixtures. Producer details are not revealed here to retain assessment neutrality. To our knowledge, none of the seeds were treated with pesticides or germination enhancers. We used an extended sowing campaign from mid-May to mid-June to minimise simultaneous survey failure due to an unpredictable period of unsuitable weather in summer.

We observed the flowering status of each treatment weekly to account for the effect of flower abundance on forage attractiveness (Sih and Baltus, 1987; Ebeling et al., 2008; Jha and Vandermeer, 2009). We recorded blooming abundance using a robust five-grade system, where three main levels form the backbone: grade one as the onset of the first flowers or the last flowers, grade three as relatively abundant blooming and grade five as the mass-flowering; the two other levels are used as intermediate states for interpretational backup and were recorded with comments for later standardisation. The relatively abundant blooming stage (grade 3) was defined by the presence of at least three blooming plants per meter of the treatment section. The mass-flowering stage (grade 5) indicated that most plants were in bloom (in species-rich mixtures this was observed at least in the upper layer). This grading approach was considered optimal because the experiment consisted of plant species with very different flower sizes, inflorescence structures and plant heights, meaning that detailed estimates of flower display areas or number of flower units would have been very challenging to estimate and would have had a large error rate (which we found in preliminary trials). Furthermore, frequent counting (e.g., weekly) of flowers would have imposed an enormous extra work burden.

The foraging activity of pollinators was monitored once per week in sunny or partially cloudy conditions; rainy or very overcast conditions were avoided. The main monitoring time was between 12:00 and 17:00. We tested the optimal survey timing in preliminary trials during the two years prior to the experiment, and also made occasional repeat surveys of the same experimental sites, at earlier or later times of the same day. All assessments indicated lower activity of all pollinators outside the main survey time (unpublished data). Each 10 m section of the strip was surveyed for three to five minutes with slow movement along the strip, and pollinators that made contact with a flower or inflorescence were counted as visitors. Longer observation of the same strip section would have caused repeat counting of the same pollinator moving between flowers.

We monitored three groups of insect pollinators on flowers: (i) honey bees (*Apis mellifera*), (ii) bumblebees (mostly *Bombus* spp.), and (iii) other (conspicuous) pollinators. The group of other pollinators (labelled as such for simplicity of reading) consisted mostly of visually-conspicuous taxonomic groups, such as hoverflies (*Syrphidae*), larger

**Table 1**

Landscape composition within a 3 km radius of study sites with 50-percentile range of observations.

| Land-cover type                 | 25-percentile | Average | 75-percentile |
|---------------------------------|---------------|---------|---------------|
| Crop land                       | 27.4          | 32.6    | 42.6          |
| of which summer-flowering crops | 1.7           | 4.0     | 5.0           |
| Forest and shrub land           | 23.3          | 34.9    | 47.9          |
| Gardens, yards                  | 6.9           | 17.8    | 16.0          |
| Wetlands                        | 0.3           | 1.3     | 1.6           |



solitary bees (*Apoidea*, except *Apis* and *Bombus*) and butterflies (*Lepidoptera*), which are native pollinator of many flower species. Species determination was not performed as this was unnecessary for assessing the functional intensity (attractiveness to forage) of flower areas. Honey bees were addressed separately as they are the main target group of the flower-field agri-environmental measure (one of the driving reason of the present study) and as they are a domesticated pollinator species whose abundance in landscapes is highly regulated. Bumblebees are (still) regionally abundant in Estonia (Mänd et al., 2002; Söber et al., 2020). We selected bumblebees to characterize the responses of wild social pollinators, which are generally polylectic and have wide foraging ranges and low dependency on landscape structure (Beekman and Ratnieks, 2000; Steffan-Dewenter et al., 2002; Westphal et al., 2006; Greenleaf et al., 2007), with some exceptions (Rundlöf et al., 2008; Kennedy et al., 2013; Scheper et al., 2015). The group of other conspicuous pollinators was included to characterize the potential responses of mostly solitary pollinators in annual flower fields, though it is clear that the group is very heterogeneous.

The field survey at each specific site ended either following destruction of the strip as a result of crop management in the field, or the arrival of unsuitable weather conditions for bees and plants in late autumn. In 2021, there was an exceptionally warm autumn, and honey bees were actively foraging at still blooming experimental sites on the 2nd of November (a partly sunny day with no wind, 5–7 °C at midday and frost at night). Evidently, in autumn, honey bee foraging activity is mostly limited by a lack of late-flowering forage plants and less by temperature. In 2022, unsuitable weather started already in the end of September. Altogether, the survey period at different sites varied from a few weeks up to thirteen weeks; on average the pollinator survey was performed during seven weeks per site.

## 2.2. Data analysis

Weeks with at least relatively abundant flowering (grades 3–5) were extracted from the survey data. In the present experimental setting, low abundance blooming (grades 1 and 2) was a brief period in the phenology of these flower rich communities, which can be considered as data noise where the rare observation of visiting insect pollinators is not indicative of service provision. The number of weeks with abundant flowering was estimated and was analysed as an indicator of the functional stability of services provided by flowers. The functional intensity of the service provided by the flower community was described with the number of flower visiting specimens recorded for each pollinator group per 10 m treatment section. In the analyses of flower visiting activity, we used observations only until the end of August, as this is the main foraging period of honey bees and bumblebees (Carreck and Williams, 1997; von Königslöw et al., 2022). This also reflects the period of flower-area maintenance prescribed by the agri-environmental contract; from the end of August many bee keepers start to provide complementary syrup for honey bees, and flower visiting estimates might become biased as a result. Finally, we summed the counts of visitors per treatment within each group for the whole season to obtain pooled seasonal visiting activity estimates.

Most response variables in the data set were analysed using general linear mixed model analysis (procedure MIXED) in SAS ver 9.4 (Littell et al., 1996) as the model residuals were normally distributed, except the

data for the group of other conspicuous pollinators. Their weekly activity counts were very low, and predicted estimates of averages too close to zero. Therefore we used generalized linear mixed model (procedure GLIMMIX in SAS ver 9.4) with negative binomial error-distribution and log-link function, although the error distribution was best fitted by a normal distribution; but as model test results had minor differences the negative binomial was chosen because of more reasonable distribution of prediction variability asymmetry. For the general mixed models, response variables were log-transformed prior to analysis to remove multiplicative effects between factors. In the results, we refer to both approaches as mixed model.

We performed analysis at two levels of treatment classification. First, in the ‘model for theory’ we tested hypotheses about the effect of the diversity gradient, i.e. species-specific treatments with the same diversity level were pooled. Specifically, we pooled monocultures (labelled as ‘Mono’) and variants of the high-diversity mixture with the dominant forage species (labelled as ‘Dom-mix’) (Table 2). Secondly, in the ‘model for practice’, we estimated variability between all eight original treatment levels, i.e., at forage species level, to test diversity effects within flower-species based gradients, and on the assumption that such detailed information has applied value for farmers.

In models of foraging activity of insect pollinators, we included a factor ‘GrowthWeek’ – the number of weeks since sowing at the site – to account for the phenological stage of plants. Both factors (diversity level or treatment) and growing week were also provided with the interaction term of ‘Year’ to account for possible differences in effects between years – note that it was not the aim of the study to estimate annual differences; rather, the factor was included to account for potential temporal confounding. To ensure the robustness of the fixed part of model, we tested the effects of some landscape properties (Table 1) and the distance from the nearest hive in the models; however, their systematic effects were not statistically significant, and they were not included in the final set of analyses. Tukey’s HSD multiple comparison test was used to interpret differences between treatment levels when the overall effect in a model was significant.

In all models, we considered experimental ‘Site’ as a random factor to account for variability created by site-specific conditions, such as the abundance of pollinators in the landscape, landscape context, neighbouring crops, soil type, crop and field management and local specificity of seasonal weather. Interaction terms ‘Site\*GrowthWeek’ and ‘Site\*Treatment’ were included to account for the underestimation of variability caused by repeated observations at each site.

## 3. Results

### 3.1. Flowering duration

The abundant flowering period (flower abundance grades 3–5) of monocultures was slightly more than a week shorter than any of the mixtures (Table 3A) (Fig. 1A). The low-diversity mixture and all types of high-diversity mixture had equivalently long-duration flowering, until the autumn frost or until the experimental strip was destroyed by management. The ‘model for practice’ (Table 3B) confirmed the systematically shorter flowering period of monocultures, and showed that the low-diversity mixture (consisting of the three forage species) had equivalent continuation of flowering to the high-diversity mixtures

**Table 2**  
Diversity levels, specific sowing treatments and their labels used in the experiment and analysis.

| Diversity level                      | Diversity code | Sowing treatments    |                                      |                        |
|--------------------------------------|----------------|----------------------|--------------------------------------|------------------------|
| Monoculture                          | Mono           | Borage (BO)          | Cornflower (CC)                      | Phacelia (PT)          |
| Low-diversity mixture                | Low-div        |                      | Borage + Cornflower + Phacelia (BCT) |                        |
| High diversity mixture with dominant | Dom-mix        | Borage + mix (BOMix) | Cornflower + mix (CCmix)             | Phacelia + mix (PTmix) |
| Balanced high diversity mixture      | High-div       |                      | High-diversity mixture (mix)         |                        |



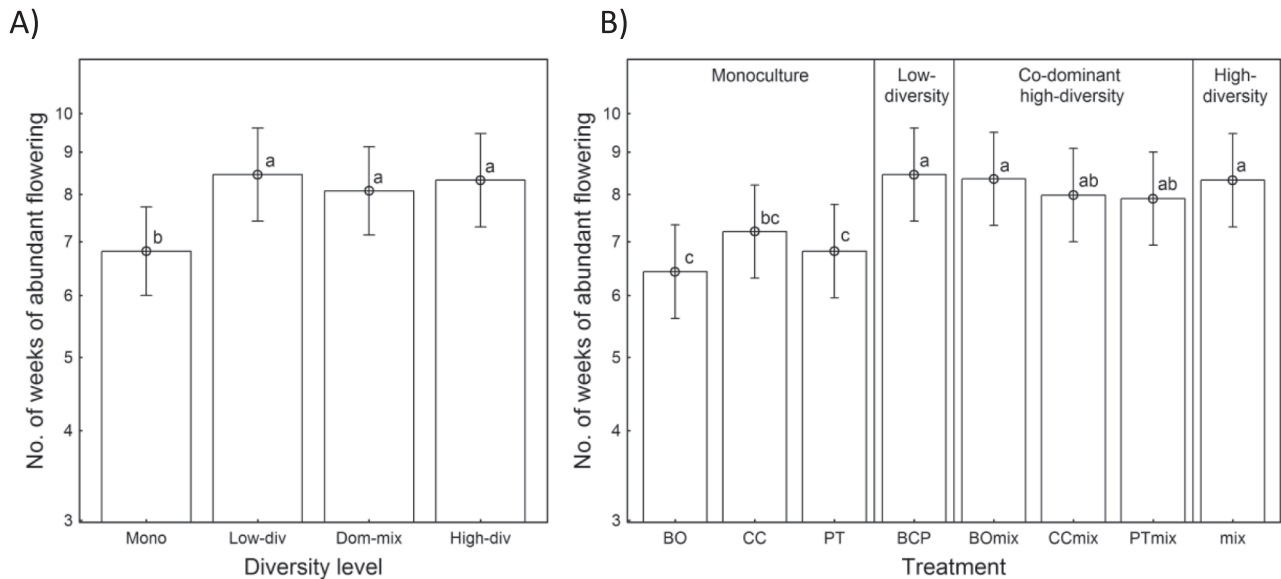
**Table 3**

Results of mixed models estimating the effects of year (Year) and diversity gradient (DiversityLevel) on the number of weeks of abundant flowering and on the cumulative counts of honey bees, bumblebees and other conspicuous pollinators over the season (the ‘model for theory’). In the ‘model for practice’, the factor DiversityLevel (four diversity levels) is replaced with the factor Treatments (eight diversity treatment types). Site is considered as a random factor.

| A) Model for theory  |        | Flowering weeks |               | Honey bees   |               | Bumblebees   |               | Other pollinators |               |
|----------------------|--------|-----------------|---------------|--------------|---------------|--------------|---------------|-------------------|---------------|
| Fixed effect         | df     | F-value         | P-level       | F-value      | P-level       | F-value      | P-level       | F-value           | P-level       |
| Year                 | 1; 224 | 1.97            | 0.1619        | <b>16.91</b> | <b>0.0001</b> | 1.36         | 0.2447        | 2.78              | 0.0964        |
| DiversityLevel       | 3; 224 | <b>31.13</b>    | <b>0.0001</b> | <b>77.69</b> | <b>0.0001</b> | <b>42.68</b> | <b>0.0001</b> | <b>3.86</b>       | <b>0.0099</b> |
| DiversityLevel*Year  | 3; 224 | 0.25            | 0.8604        | <b>5.16</b>  | <b>0.0018</b> | 1.25         | 0.2916        | <b>2.65</b>       | <b>0.0494</b> |
| Covariance structure |        | Z-value         | P-level       | Z-value      | P-level       | Z-value      | P-level       | Z-value           | P-level       |
| Site                 |        | 3.85            | 0.0001        | 3.61         | 0.0002        | 3.47         | 0.0003        | 3.28              | 0.0005        |
| Residual or Scale    |        | 10.58           | 0.0001        | 10.58        | 0.0001        | 10.58        | 0.0001        | 7.18              | 0.0001        |

| B) Model for practice |        | Flowering weeks |               | Honey bees   |               | Bumblebees   |               | Other pollinators |               |
|-----------------------|--------|-----------------|---------------|--------------|---------------|--------------|---------------|-------------------|---------------|
| Fixed effect          | df     | F-value         | P-level       | F-value      | P-level       | F-value      | P-level       | F-value           | P-level       |
| Year                  | 1; 216 | 2.07            | 0.1516        | <b>19.15</b> | <b>0.0001</b> | 1.24         | 0.267         | 2.54              | 0.1125        |
| Treatment             | 7; 216 | <b>15.25</b>    | <b>0.0001</b> | <b>40.54</b> | <b>0.0001</b> | <b>38.47</b> | <b>0.0001</b> | <b>10.12</b>      | <b>0.0001</b> |
| Treatment*Year        | 7; 216 | 0.19            | 0.9869        | <b>2.58</b>  | <b>0.0144</b> | 1.41         | 0.2006        | <b>2.18</b>       | <b>0.0366</b> |
| Covariance structure  |        | Z-value         | P-level       | Z-value      | P-level       | Z-value      | P-level       | Z-value           | P-level       |
| Site                  |        | 3.85            | 0.0001        | 3.64         | 0.0001        | 3.6          | 0.0002        | 3.42              | 0.0003        |
| Residual or Scale     |        | 10.39           | 0.0001        | 10.39        | 0.0001        | 10.39        | 0.0001        | 6.34              | 0.0001        |



**Fig. 1.** The number of weeks of abundant flowering in different flower-strip treatments. Whiskers represent 95%-confidence intervals. Labels above bars denote homogenous groups according to Tukey's multiple comparison test. Diversity levels in (A): Mono – monoculture, Low-div – low-diversity mixture of the three species used in monoculture, Mono-mix – combination of the high-diversity mixture with a dominant forage species, High-div – high-diversity seed mixture with relatively balanced abundances. Treatment codes in (B): BO, CC and PT – monocultures of borage, cornflower and phacelia, respectively, BCP – low-diversity mixture of the three species, BOmix, CCmix and PTmix – combination of the high-diversity mixture with a dominant forage species, mix – the high-diversity mixture. Cross-tabulation of codes see Table 2.

(Fig. 1B). Thus, the three-species mixture was sufficient to ensure long continuity of abundant flowering, i.e. flower service stability.

### 3.2. Foraging activity – General information

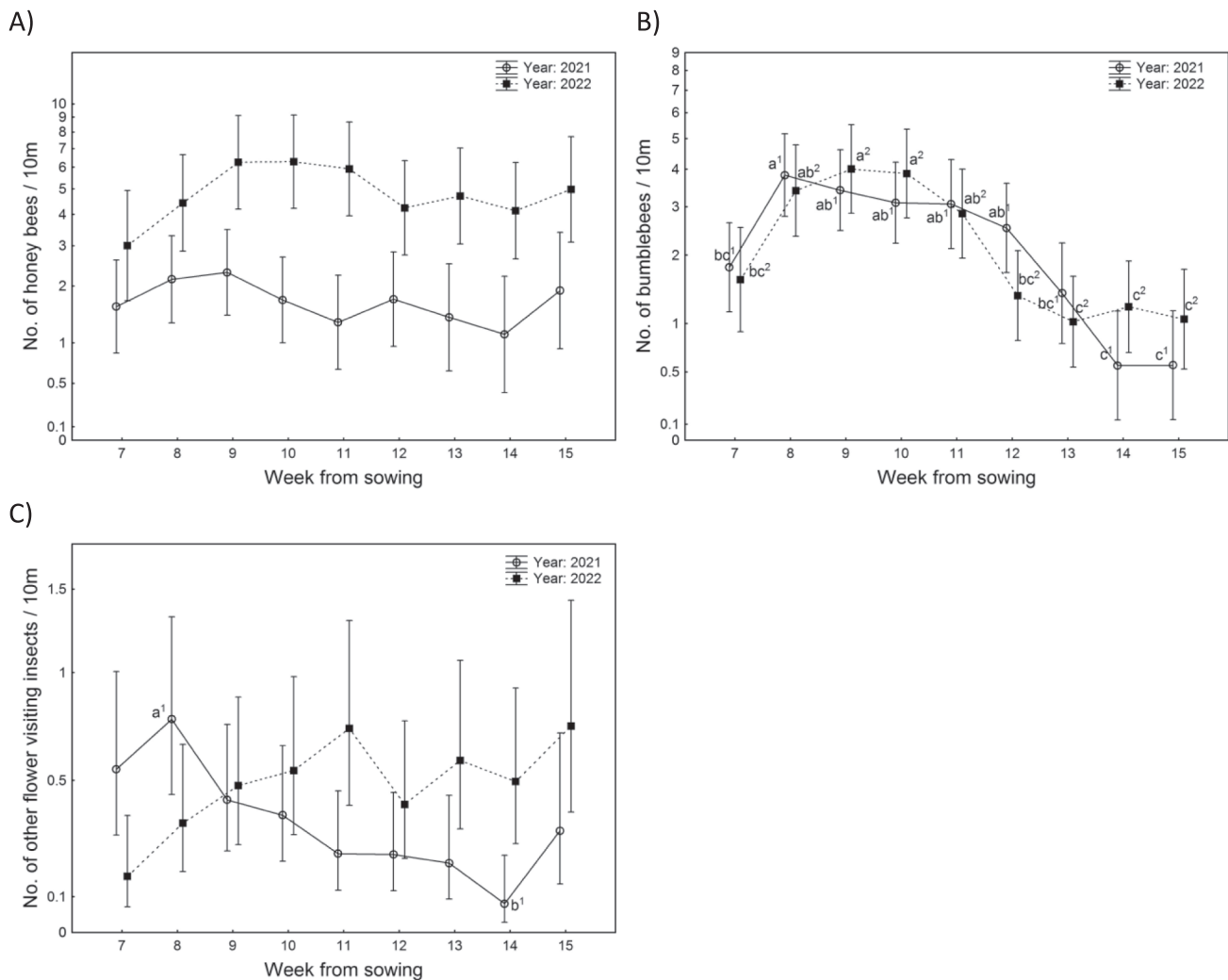
The average number of flower visitors per treatment section (foraging activity) was quite low (Fig. 2); however, there were peaks in some sites or some weeks. For instance, the 90-percentile of honey bee count was 18 specimens per 10 m section, but the maximum count was around 100 specimens per 10 m section (more details Fig. S4). The upper estimates for bumblebees were also surprisingly high: the 90-percentile was 11 specimens per 10 m treatment section, and the largest count was 60 specimens per 10 m section. Other pollinators were scarcer: the 90-percentile was 3 specimens, and the maximum was 16 specimens per 10 m section.

Honey bees and bumblebees had different phenological patterns of foraging activity (Fig. 2; factors GrowthWeek and Year and their interaction in Table 4). The number of honey bees was relatively uniform during each summer, but the counts differed between years (Fig. 2A). Note, as sites largely do not overlap, the effect of the year can be site-specific. By contrast, bumblebees had a unimodal activity pattern, with the maximum number of flower visiting specimens in July; and their counts and phenological patterns of foraging activity were similar between years (Fig. 2B). The visiting activity of other pollinators was too low to detect general trends within and between years (Fig. 2C).

### 3.3. Foraging activity – The model for theory

According to the ‘model for theory’, the diversity level had a systematic effect (Table 4A). The average number of honey bees per survey





**Fig. 2.** Average number of honey bees (A), bumblebees (B) and other conspicuous pollinators (C) during the abundant flowering season in two years. Whiskers represent 95%-confidence intervals. Labels next to points denote homogenous groups according to Tukey's multiple comparison test; the superscript numeral indicates the year for which the difference was tested.

was uniformly high in monocultures and in the low-diversity mixture (Fig. 3A). The high-diversity mixture with the dominant forage species was characterised by intermediate counts of honey bees, while the balanced high-diversity mixture was visited least frequently. The greatest number of bumblebees foraged in the low-diversity mixture with only slightly fewer in monocultures (Fig. 3B). The number of bumblebee specimens was clearly lower in the high-diversity mixtures with dominant flower species and lowest in the balanced high-diversity mixture. Other conspicuous flower visitors were overall characterised by low numbers of specimens, but there were hints of analogous differences in activity counts in relation to the diversity gradient – higher in monocultures and lower in the balanced high-diversity mixture (Fig. 3C).

Cumulative number of visitors over the season mirrored patterns of average activity per survey for all three pollinator groups (Fig. S5) and there were mostly systematic differences between years (Table 3A, Table 4A).

### 3.4. Foraging activity – The model for practice

In the detailed analyses of treatment effects, honey bees and bumblebees exhibited preferences for different forage plant species (Table 4B), but the systematic suppressive effect of diversity on foraging

activity was consistent in relation to all three plant species (Fig. 4). The number of honey bees was greatest in the borage monoculture, and similar in cornflower, phacelia and the three-species mixture (Fig. 4A). Bumblebees preferred to forage on phacelia and the low-diversity mixture, and to an extent also in the phacelia dominated high-diversity mixture. Bumblebees visited the monocultures of borage and cornflower less frequently (Fig. 4B), but their foraging activity in the high-diversity mixture with the respective plant species present as dominants was still systematically lower. The balanced high-diversity treatment got the lowest visiting activity from both groups of bees. Other conspicuous pollinators had highest counts in the monocultures of cornflower and phacelia. Their lowest activity was observed in the monoculture of borage, the borage dominated high-diversity mixture and the balanced high-diversity mixture (Fig. 4C), while activity in other treatments was intermediate and fitted into the general pattern along the plant diversity gradient.

The pattern of honey bee foraging activity in forage species-specific treatments was similar in both years (Table 4B), though the diversity effect was more evident in the second year (Fig. S6A), when the overall activity of honey bees was higher (Fig. 2). Bumblebees showed a very similar response to the treatments in both years (Fig. S6B). As other pollinators had very low foraging activity rates in all treatments, estimates of yearly variation in response to the treatments were imprecise



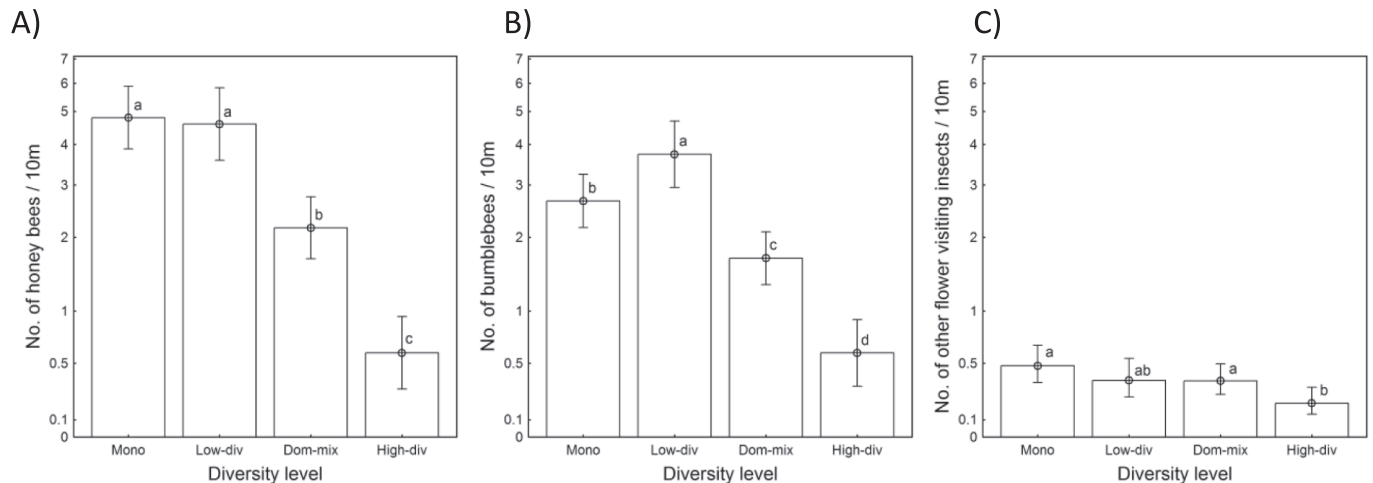
**Table 4**

Results of mixed models estimating the effect of year (Year), the number of weeks since the sowing date (GrowthWeek) and the diversity gradient (DiversityLevel) on the average number of honey bees, bumblebees and other conspicuous pollinators in weekly surveys of 10 m sections (in the 'model for theory'). In the 'model for practice', the factor DiversityLevel (four diversity levels) is replaced with a factor Treatments (eight diversity treatment types). Site and random factors are included to account for the repeated nature of observations.

| A) Model for theory  |         | Honey bees    |               | Bumblebees   |               | Other pollinators |               |
|----------------------|---------|---------------|---------------|--------------|---------------|-------------------|---------------|
| Fixed effect         | df      | F-value       | P-level       | F-value      | P-level       | F-value           | P-level       |
| Year                 | 1; 1565 | <b>20.21</b>  | <b>0.0001</b> | 0.23         | 0.6335        | 2.58              | 0.1081        |
| GrowthWeek           | 8; 196  | 1.86          | 0.0676        | <b>23.78</b> | <b>0.0001</b> | 1.56              | 0.1315        |
| GrowthWeek*Year      | 8; 1565 | 1.14          | 0.335         | <b>2.14</b>  | <b>0.0299</b> | <b>4.48</b>       | <b>0.0001</b> |
| DiversityLevel       | 3; 1565 | <b>116.08</b> | <b>0.0001</b> | <b>51.21</b> | <b>0.0001</b> | <b>6.68</b>       | <b>0.0002</b> |
| DiversityLevel*Year  | 3; 1565 | <b>12.51</b>  | <b>0.0001</b> | 1.55         | 0.1996        | 1.99              | 0.1133        |
| Covariance structure |         | Z-value       | P-level       | Z-value      | P-level       | Z-value           | P-level       |
| Site                 |         | 3.09          | 0.001         | 2.88         | 0.002         | 2.73              | 0.0031        |
| Site*GrowthWeek      |         | 7.55          | 0.0001        | 6.34         | 0.0001        | 4.85              | 0.0001        |
| Site*Treatment       |         | 5.73          | 0.0001        | 6.69         | 0.0001        | 3.87              | 0.0001        |
| Residual or Scale    |         | 25.95         | 0.0001        | 25.9         | 0.0001        | 6.56              | 0.0001        |

| B) Model for practice |         | Honey bees   |               | Bumblebees   |               | Other pollinators |               |
|-----------------------|---------|--------------|---------------|--------------|---------------|-------------------|---------------|
| Fixed effect          | df      | F-value      | P-level       | F-value      | P-level       | F-value           | P-level       |
| Year                  | 1; 1557 | <b>22.47</b> | <b>0.0001</b> | 0.01         | 0.914         | 2.41              | 0.1205        |
| GrowthWeek            | 8; 196  | 1.81         | 0.0769        | <b>23.43</b> | <b>0.0001</b> | 1.65              | 0.1065        |
| GrowthWeek*Year       | 8; 1557 | 1.13         | 0.3376        | <b>2.2</b>   | <b>0.0251</b> | <b>5.53</b>       | <b>0.0001</b> |
| Treatment             | 7; 1557 | <b>67.55</b> | <b>0.0001</b> | <b>67.08</b> | <b>0.0001</b> | <b>11.63</b>      | <b>0.0001</b> |
| Treatment*Year        | 7; 1557 | <b>6.53</b>  | <b>0.0001</b> | 1.71         | 0.1027        | 1.78              | 0.0866        |
| Covariance structure  |         | Z-value      | P-level       | Z-value      | P-level       | Z-value           | P-level       |
| Site                  |         | 3.15         | 0.0008        | 3.12         | 0.0009        | 2.90              | 0.0007        |
| Site*GrowthWeek       |         | 7.55         | 0.0001        | 6.38         | 0.0001        | 4.84              | 0.0001        |
| Site*Treatment        |         | 4.62         | 0.0001        | 3.56         | 0.0004        | 2.43              | 0.0005        |
| Residual or Scale     |         | 25.94        | 0.0001        | 25.9         | 0.0001        | 6.63              | 0.0001        |



**Fig. 3.** Average count of flower visitors per survey in 10 m section (foraging activity rate) of honey bees (A), bumblebees (B) and other conspicuous pollinators (C) per survey in flower strips with different diversity levels. Whiskers represent 95%-confidence intervals. Labels above bars denote homogenous groups according to Tukey's multiple comparison test. Diversity levels: Mono – monoculture, Low-div – low-diversity mixture of the three species used in monocultures, Mono-mix – combination of the high-diversity mixture with a dominant forage species, High-div – high-diversity mixture (Table 2).

(Fig. S6C) and the interaction effect non-significant. Cumulative counts per season (Table 3B) reflected patterns of weekly activities (Fig. S7).

## 4. Discussion

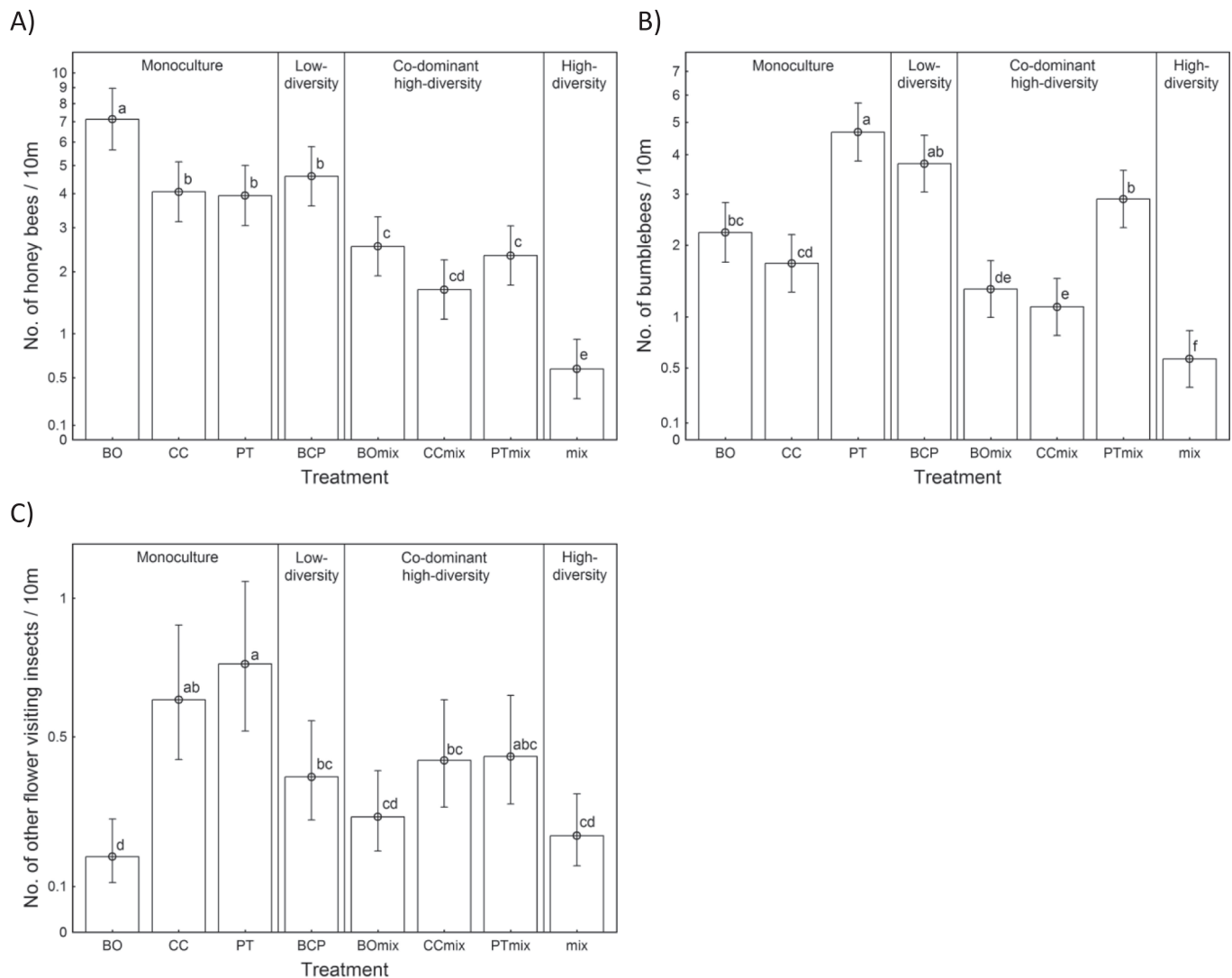
### 4.1. Theoretical aspects

The role of biodiversity in shaping the provisional quality of ecosystem services is still debated (Cardinale et al., 2011; Balvanera et al., 2014). We focussed on floral services provided by plants, and specifically addressed the service of a forage source for bees and other conspicuous insect pollinators. This service forms the basis for a hierarchy of ecological interactions and should result in increased honey

production and improved pollination of crops. The agri-environmental measure and eco-scheme contract in Estonia is designed based on this logic. Testing hypotheses about the plant diversity effect on floral service quality, we recorded different support concerning the shape of the response curve, depending on the service quality aspect. We observed the expected positive non-linear relationship between plant diversity and the duration of flowering of the plant community (interpreted as service stability). However, we found unexpected evidence that increasing plant diversity can cause a reduction of foraging activity among insect pollinators, i.e. the realized attractiveness and service provision intensity of flowers declined.

The duration and stability of ecosystem service provision are important features to assess, but they do not always determine the





**Fig. 4.** Average count of flower visitors per survey in 10 m section (foraging activity rate) of honey bees (A), bumblebees (B) and other conspicuous pollinators (C) during the abundant flowering period in different treatments. Whiskers represent 95%-confidence intervals. Labels above bars denote homogenous groups according to Tukey's multiple comparison test. Treatment codes: BO, CC and PT – monocultures of borage, cornflower and phacelia, respectively, BCP – low-diversity mixture of the three species, BOmix, CCmix and PTmix – combination of the high-diversity mixture with a dominant forage species, mix – high-diversity mixture (Table 2).

overall quality of service provision (Kütt et al., 2018). We observed that the extended duration of flowering in high-diversity mixtures had its maximum limit dictated by external factors, such as the end of the growing season and farming activities, which means that the realized functional stability of the flower service saturated already at the low diversity level. Long-duration blooming until the end of the growing season is rarely suitable for farming practices as bee-crops are usually used for intercropping – a short-term application until the sowing of winter crops. Analogous external limitation of active flowering occurs in grassland where the early or mid-season mowing interrupts the flowering of many plants, independent of the species diversity level. The ecological benefit of long-duration blooming is also limited by the seasonality of pollinators, which, in this study, was particularly evident for bumblebees. The activity period of domesticated honey bees is determined by bee keepers, who, in Estonia, typically provide complementary syrup from late August. In the future, when warm autumns will occur more frequently due to climate change, honey bees might profit more from the seasonally extended flower service after the winter feed processing has been completed. Other wild pollinators (solitary bees, syrphids, butterflies) are probably the main beneficiaries of season-long-flowering in fields, as they continuously foraged until the frosts;

however, their abundances were too low in agriculture dominated landscapes for such a policy measure to be reasonably efficient.

The direction and shape of the response curve of foraging activity in relation to plant diversity was very different from the one we proposed in working Hypothesis 1 – we observed a clear decline in the counts of flower visitors towards high-diversity flower mixtures, rather than the expected positive levelling-out response (Tilman et al., 1997; Loreau et al., 2001). Evidently, species-poor communities can be functionally more effective than diverse flower communities and that flower visiting insect pollinators are more attracted to forage in simple flower communities. Moreover, this was largely consistent between insect pollinator groups. Honey bees and bumblebees, as species with social and cooperative foraging behaviour (Carreck and Williams, 1997; Goulson 1999; Rundlöf et al., 2018), were clearly more attracted to low-diversity treatments: either monocultures or a three-species mixture. We also expected to find that wild solitary pollinators are scattered between and within resource rich treatments because of their individual behaviour (Sih and Baltus, 1987; Ebeling et al., 2008; Jha and Vandermeer, 2009). However, our observations suggest that if solitary species have an option to choose between forage sites at the local scale, they may still prefer low-diversity habitats or monocultures where forage plants are in



abundance. The general suppressive effect of flower diversity received additional support from Hypothesis 2, as the alternative outcome was recorded – co-occurring diversity suppressed the service intensity provided by a (co-)dominant species in monoculture. The resulting service intensity of the treatment was thus more similar to the high diversity treatment. The suppressive effect of high floral diversity was systematically evident for all three paired sets of main forage plant species, though it was not as clear for the group of other conspicuous pollinators. The suppressed foraging activity of honey bees and bumblebees can be explained by the sensitivity of social pollinators to the extra energy effort required to forage in diverse flower communities (Kacelnik et al., 1986; Goulson 1999; Cartar 2004). They focus on resource-rich patches (Hegland and Totland, 2005; Venjakob et al., 2016; Marja et al., 2018) or even on one resource rich plant species at a time to optimise the ‘energetic efficiency gain’ during resource acquisition (Carreck and Williams, 1997; Goulson 1999; Rundlöf et al., 2018). In studies where social bees have been shown to be attracted to species-rich habitats, frequently these flower-rich communities have been compared with habitats characterized by low flower abundance, by specific flowering-reducing management regimes and/or different habitat types in different landscape contexts (Carvell et al., 2007; Ebeling et al., 2008; Scheper et al., 2021).

The foraging activity of bees has been shown to decline in the presence of co-flowering species with contrastingly different floral properties (Fornoff et al., 2017); a process known as functional isolation or structural distraction (Kunin 1993; Otto et al., 2017; Albor et al., 2019). By contrast, mixtures of close relative species or species with similar floral features tend to facilitate each other and attract pollinators (Kunin 1993; Hegland and Totland, 2005; Ghazoul 2006). In this experiment, the three main forage species used in the low-diversity mixture were taxonomically and morphologically dissimilar, except for their common bluish-lilac flower colour. In their mixture, however, we did not observe any specific distraction effect or synergy on the foraging activity of honey bees and bumblebees, as the estimates were similar to those observed in monocultures. Even if each insect pollinator group had a slight preference for a certain forage plant species (honey bees for borage, bumblebees for phacelia and other pollinators for cornflower and phacelia), foraging activity in the three species mixture was almost the average of the activities recorded in the monocultures. This shows that low-diversity mixtures, where all species are abundant, can be functionally effective in service provision intensity, and at the same time these few flower species can complement each other in terms of phenology and increase the service duration or stability.

#### 4.2. Implications

Functional saturation has also been noted in the some specific studies on plant-pollinator relationships (Ghazoul 2006; Hegland and Boeke, 2006; Ebeling et al., 2008; Rundlöf et al., 2018), but this knowledge is rarely reflected in policy and ecological applications. Flower-rich mixtures are advertised to be effective, but they seem to be poorly optimized to attract insect pollinators to forage (Carreck and Williams, 1997; Otto et al., 2017; Scheper et al., 2021), and their flower diversity and long-duration blooming has rather been targeted towards public appreciation (i.e. an aesthetic service) (Junge et al., 2009; Lindemann-Matthies and Marty, 2013). However, human perception of service provision quality cannot be linearly transferred onto other flower service user groups (Carreck and Williams, 1997; Hoyle et al., 2018; Kütt et al., 2018). We showed that flower mixtures can be highly effective when composed of only a few true bee-forage plant species that are morphologically, functionally and phenologically complementary. We suggest that pollinator-oriented seed mixtures should be quantitatively tested to determine the efficiency of the ecological service that they aim for, and that plant species lists should be mandatory on seed packages.

Flower-field or bee-crop species mixtures and field management methods should also focus on optimization of blooming phenology (e.g.

sequential flowering) to reduce competition for pollinator attention (Carvell et al., 2007; Albor et al., 2019; Scheper et al., 2021). Specifically, bee-crops should be targeted on periods when there is a seasonal gap in nectar availability in the landscape (Timberlake et al., 2019; von Königsłow et al., 2022), and avoid competition with mass-flowering production crops (Holzschuh et al., 2011; Grab et al., 2017). Blooming niche differentiation is common in natural flower communities (Albor et al., 2020; Su et al., 2022). The blooming of monocultures, which was only a week or two shorter than mixtures, can provide the same service stability by growing different monocultures with different flowering phenologies or by differentiating the repeated sowing times of the same species (Albor et al., 2020). Growing monocultures can avoid competition between plant species for soil and light resources and allows flexible management of each flower species from sowing to seed collection (Martins et al., 2018). Low-diversity mixtures flowering at the optimal time, e.g. in autumn, can also be appreciated by the public as a high quality aesthetic service (Hoyle et al., 2018).

Optimisation of ecosystem service provision over multiple spatial and temporal scales is a highly complex exercise (Hein et al., 2006; Geijzendorffer and Roche, 2014). Wild pollinators are expected to profit from agri-environmental measures designed to support domestic honey bees (Potts et al., 2010; Kleijn et al., 2018; Hall and Martins, 2020). Yet, annual short-term agri-environmental measures cannot effectively support all potential pollinators (Blaauw and Isaacs 2014; Wood et al., 2015; Martins et al., 2018). We showed that bumblebees would profit from measures optimal for domestic honey bees, while many wild solitary pollinators were unable to react efficiently to the short-term appearance of man-made forage habitats in the same way, or they had low abundance in general. Many studies in agricultural landscapes have struggled with the low abundance of wild solitary pollinator species, explained by their short dispersal range, high site fidelity (Albrecht 2003; Ricketts et al., 2008; Wood et al., 2015) and heavy dependence on landscape context, such as the availability of permanent undisturbed natural habitats (Steffan-Dewenter et al., 2002; Alanen et al., 2011; Wix et al., 2019). Short-term forage areas as a policy measure should be targeted to the needs of wide-ranging insect pollinators such as honey bees and bumblebees, which can react to annual resource fluxes in agriculture-dominated landscapes. Wide support for all kinds of pollinator community might only be achieved by combined application of different agri-environmental measures, resulting in a multi-functional landscape mosaic containing both permanent (semi-)natural habitats and mass-flowering fields (Menz et al., 2011; Tonietto and Larkin, 2018; Garibaldi et al., 2021; von Königsłow et al., 2022). Using a mosaic of monoculture fields, fields with low-diversity mixtures, or even cultivation of flower monocultures in a strip-crop field-system might be the most convenient methods. In such a mosaic landscape, the presence of bee-crop areas could leave (semi-)natural grasslands out of the scope of domestic bees, leaving these habitats for more sensitive wild pollinators (Quinlan et al., 2021; Toivonen et al., 2022). A specific flower-field version tested in the future might be autumn flowering south-facing quick-snack patches near beehive groups or fragments of (semi-)natural habitat.

The assessment and monitoring of policy measures should also be updated. Plant species diversity is a standard indicator implemented into various methods for assessing agricultural policy measures or habitat monitoring schemes (Balvanera et al., 2006; Isbell et al., 2011; Elmiger et al., 2023). Biodiversity can be a confusing or at least non-linear indicator of other functional or structural components of the ecosystem (Billeter et al., 2008), and some of these ecological relationships conflict with general expectations about a uniform positive effect of biodiversity. We suggest the planning of policy measures and the programs monitoring the efficiency of agri-environmental programs should be re-evaluated, in particular where measuring the functional quality of (restored) ecosystems is a main aim. This is particularly important in the design of results-based payments in agri-environmental schemes, where biodiversity is considered one of the best target



indicators (Balvanera et al., 2006; Isbell et al., 2011; Herzon et al., 2018; Elmiger et al., 2023). The use of biodiversity as a sole, universal proxy indicator should be complemented with the implementation of specific functional properties of the ecosystem. In particular, the monitoring of specific insect taxa or pollinator groups relevant to provision intensity should be included.

## 5. Conclusions

Measuring the foraging activity of insect pollinators along an experimental gradient in plant diversity we showed that service provision quality might not be uniformly predicted by plant diversity. Flower diversity enhanced the service provision duration, but such stability had external limitations and pollinators rarely had an opportunity to benefit from it. The functional efficacy of a flower community in terms of realized foraging activity on flowers, however, was negatively correlated with the flower species diversity. Honey bees and bumblebees preferred monocultures and low diversity mixtures. Flower diversity confused foraging insect pollinators when there was a high diversity of neighbouring flower species. Honey bees are an underappreciated and potentially convenient indicator group for the assessment of flower based services (Sabbahi et al., 2005; Lindström et al., 2016; Breeze et al., 2019). Last but not least, we suggest that the proposed experimental methodology should be applied to all seed mixtures prior to be marketed with the label of a specific ecological service value.

## CRedit authorship contribution statement

**J. Liira:** Conceptualization, Methodology, Validation, Formal analysis. **I. Jürjendal:** Resources, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.110927>.

## References

- Alanen, E.L., Hyvönen, T., Lindgren, S., Härmä, O., Kuussaari, M., 2011. Differential responses of bumblebees and diurnal Lepidoptera to vegetation succession in long-term set-aside. *J. Appl. Ecol.* 48, 1251–1259.
- Albor, C., García-Franco, J.G., Parra-Tabla, V., Díaz-Castelazo, C., Arceo-Gómez, G., Bartomeus, I., 2019. Taxonomic and functional diversity of the co-flowering community differentially affect *Cakile edentula* pollination at different spatial scales. *J. Ecol.* 107 (5), 2167–2181.
- Albor, C., Arceo-Gómez, G., Parra-Tabla, V., Rafferty, N., 2020. Integrating floral trait and flowering time distribution patterns help reveal a more dynamic nature of co-flowering community assembly processes. *J. Ecol.* 108 (6), 2221–2231.
- Albrecht, H., 2003. Suitability of arable weeds as indicator organisms to evaluate species conservation effects of management in agricultural ecosystems. *Agr. Ecosyst. Environ.* 98, 201–211.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., O'Connor, M.I., Hungate, B.A., Griffin, J.N., 2014. Linking biodiversity and ecosystem services: Current uncertainties and the necessary next steps. *Bioscience* 64, 49–57.
- Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissière, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P.M., Szentgyörgyi, H., Westphal, C., Bommarco, R., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ* 2, e328.
- Beekman, M., Ratnieks, F.L.W., 2000. Long-range foraging by the honey-bee, *Apis mellifera* L. *Funct. Ecol.* 14, 490–496.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313 (5785), 351–354.
- Billetter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendrickx, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Mälfait, J. P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmanns, M., Simova, P., Verboom, J., van Wingerden, W.K.R.E., Zobel, M., Edwards, P.J., 2008. Indicators for biodiversity in agricultural landscapes: a pan-European study. *J. Appl. Ecol.* 45, 141–150.
- Blaauw, B.R., Isaacs, R., Clough, Y., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* 51 (4), 890–898.
- Breeze, T.D., Boreux, V., Cole, L., Dicks, L., Klein, A.-M., Pufal, G., Balzan, M.V., Bevk, D., Bortolotti, L., Petanidou, T., Mand, M., Pinto, M.A., Scheper, J., Stanisavljević, L., Stavrindes, M.C., Tscheulin, T., Varnava, A., Kleijn, D., Watkins, C., 2019. Linking farmer and beekeeper preferences with ecological knowledge to improve crop pollination. *People Nature* 1 (4), 562–572.
- Buhk, C., Oppermann, R., Schanowski, A., Bleil, R., Lüdemann, J., Maus, C., 2018. Flower strip networks offer promising long term effects on pollinator species richness in intensively cultivated agricultural areas. *BMC Ecol.* 18, 55.
- Butz Huryn, V.M., 1997. Ecological impacts of introduced honey bees. *Q. Rev. Biol.* 72, 275–297.
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I., Gonzalez, A., 2011. The functional role of producer diversity in ecosystems. *Am. J. Bot.* 98 (3), 572–592.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486 (7401), 59–67.
- Carreck, N.L., Williams, I.H., 1997. Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. *J. Agric. Sci.* 128 (4), 397–403.
- Carreck, N.L., Williams, I.H., 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *J. Insect Conserv.* 6, 13–23.
- Cartar, R.V., 2004. Resource tracking by bumble bees: responses to plant-level differences in quality. *Ecology* 85 (10), 2764–2771.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D., Nowakowski, M., 2007. Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J. Appl. Ecol.* 44, 29–40.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. *Nature* 387 (6630), 253–260.
- de Bello, F., Price, J.N., Münkemüller, T., Liira, J., Zobel, M., Thuiller, W., Gerhold, P., Götzenberger, L., Lavergne, S., Lepš, J., Zobel, K., Pärtel, M., 2012. Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93 (10), 2263–2273.
- Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Dicks, L.V., Hodge, I., Randall, N.P., Scharlemann, J.P.W., Siriwardena, G.M., Smith, H. G., Smith, R.K., Sutherland, W.J., 2014. A transparent process for “evidence-informed” policy making. *Conserv. Lett.* 7 (2), 119–125.
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W., Tschamtkke, T., 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos* 117 (12), 1808–1815.
- Elmiger, B.N., Finger, R., Ghazoul, J., Schaub, S., 2023. Biodiversity indicators for result-based agri-environmental schemes – Current state and future prospects. *Agr. Syst.* 204, 103538.
- Emmerson, M., Morales, M.B., Oñate, J.J., Batáry, P., Berendse, F., Liira, J., Aavik, T., Guerrero, I., Bommarco, R., Eggers, S., Pärt, T., Tschamtkke, T., Weisser, W., Clement, L., Bengtsson, J., 2016. How agricultural intensification affects biodiversity and ecosystem services. In: Dumbrell, A.J., Kordas, R.L., Woodward, G. (Eds.), *Advances in Ecological Research*. Academic Press, pp. 43–97.



- Evans, E., Smart, M., Cariveau, D., Spivak, M., 2018. Wild, native bees and managed honey bees benefit from similar agricultural land uses. *Agr. Ecosyst. Environ.* 268, 162–170.
- Fornoff, F., Klein, A.-M., Hartig, F., Benadi, G., Venjakob, C., Schaefer, H.M., Ebeling, A., 2017. Functional flower traits and their diversity drive pollinator visitation. *Oikos* 126 (7), 1020–1030.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J. H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschamtké, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* 339, 1608.
- Garibaldi, L.A., Oddi, F.J., Miguez, F.E., Bartomeus, I., Orr, M.C., Jobbágy, E.G., Kremen, C., Schulte, L.A., Hughes, A.C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D.G., Díaz, S., Dicks, L.V., Ellis, E.C., Goldenberg, M., Huaylla, C.A., Kuperman, M., Locke, H., Mehrabi, Z., Santibañez, F., Zhu, C.-D., 2021. Working landscapes need at least 20% native habitat. *Conserv. Lett.* 14, e12773.
- Geijzendorffer, I.R., Cohen-Shacham, E., Cord, A.F., Cramer, W., Guerra, C., Martín-López, B., 2017. Ecosystem services in global sustainability policies. *Environ. Sci. Policy* 74, 40–48.
- Geijzendorffer, I.R., Roche, P.K., 2014. The relevant scales of ecosystem services demand. *Ecosyst. Serv.* 10, 49–51.
- Ghazoul, J., 2006. Floral diversity and the facilitation of pollination. *J. Ecol.* 94 (2), 295–304.
- Goulson, D., 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology. Evol. Systemat.* 2, 185–209.
- Grab, H., Blitzer, E.J., Danforth, B., Loeb, G., Poveda, K., 2017. Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Sci. Rep.* 7, 45296.
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153 (3), 589–596.
- Haaland, C., Naisbit, R.E., Bersier, L., 2011. Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity* 4, 60–80.
- Hall, D.M., Martins, D.J., 2020. Human dimensions of insect pollinator conservation. *Curr. Opin. Insect Sci.* 38, 107–114.
- Hegland, S.J., Boeke, L., 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecol. Entomol.* 31 (5), 532–538.
- Hegland, S.J., Totland, Ø., 2005. Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia* 145 (4), 586–594.
- Hein, L., van Koppen, K., de Groot, R.S., van Ierland, E.C., 2006. Spatial scales, stakeholders and the valuation of ecosystem services. *Ecol. Econ.* 57, 209–228.
- Herzon, I., Birge, T., Allen, B., Povellato, A., Vanni, F., Hart, K., Radley, G., Tucker, G., Keenleyside, C., Oppermann, R., Underwood, E., Poux, X., Beaufay, G., Pražan, J., 2018. Time to look for evidence: Results-based approach to biodiversity conservation on farmland in Europe. *Land Use Policy* 71, 347–354.
- Holzschuh, A., Dormann, C.F., Tschamtké, T., Steffan-Dewenter, I., 2011. Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proc. R. Soc. B Biol. Sci.* 278 (1723), 3444–3451.
- Hoyle, H., Norton, B., Dunnett, N., Richards, J.P., Russell, J.M., Warren, P., 2018. Plant species or flower colour diversity? Identifying the drivers of public and invertebrate response to designed annual meadows. *Landsc. Urban Plan.* 180, 103–113.
- Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S., Loreau, M., 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477 (7363), 199–202.
- Jha, S., Vandermeer, J.H., 2009. Contrasting bee foraging in response to resource scale and local habitat management. *Oikos* 118 (8), 1174–1180.
- Jones, L., Brennan, G.L., Lowe, A., Creer, S., Ford, C.R., de Vere, N., 2021. Shifts in honeybee foraging reveal historical changes in floral resources. *Commun. Biol.* 4, 37.
- Junge, X., Jacot, K.A., Bosshard, A., Lindemann-Matthies, P., 2009. Swiss people's attitudes towards field margins for biodiversity conservation. *J. Nat. Conserv.* 17 (3), 150–159.
- Kacelnik, A., Houston, A.I., Schmid-Hempel, P., 1986. Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. *Behav. Ecol. Sociobiol.* 19 (1), 19–24.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., Anderson, M., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16 (5), 584–599.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauber, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tschamtké, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6 (1).
- Kolkman, A., Dopagne, C., Piqueray, J., 2022. Sown wildflower strips offer promising long term results for butterfly conservation. *J. Insect* 26 (3), 387–400.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10 (4), 299–314.
- Kunin, W.E., 1993. Sex and the Single Mustard: Population Density and Pollinator Behavior Effects on Seed-Set. *Ecology* 74, 2145–2160.
- Kütt, L., Lohmus, K., Ramm, I.-J., Paal, T., Paal, J., Liira, J., 2016. The quality of flower-based ecosystem services in field margins and road verges from human and insect pollinator perspectives. *Ecol. Ind.* 70, 409–419.
- Kütt, L., Paal, T., Lohmus, K., Ramm, I.-J., Zobel, K., Liira, J., Vandvik, V., 2018. Multi-user quality of floral services along a gradient of margin habitats between semi-natural grasslands and forests. *Appl. Veg. Sci.* 21 (3), 363–372.
- Liira, J., Trisberg-Uljas, T., Karofeld, E., Karu, H., Paal, J., 2019. Does the autecology of core species reflect the synecology of functional groups during the assembly of vegetation in abandoned extracted peatlands? *Mire Peat* 28, 1–14.
- Lindemann-Matthies, P., Marty, T., 2013. Does ecological gardening increase species richness and aesthetic quality of a garden? *Biol. Conserv.* 159, 37–44.
- Lindström, S.A.M., Herbertsson, L., Rundlöf, M., Smith, H.G., Bommarco, R., 2016. Large-scale pollination experiment demonstrates the importance of insect pollination in winter oilseed rape. *Oecologia* 180 (3), 759–769.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS® system for mixed models. SAS Publishing, Cary, NC, USA.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294 (5543), 804–808.
- Mallinger, R.E., Gaines-Day, H.R., Gratton, C., Raine, N.E., 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLoS One* 12 (12), e0189268.
- Mänd, M., Mänd, R., Williams, I.H., 2002. Bumblebees in the agricultural landscape of Estonia. *Agr. Ecosyst. Environ.* 89, 69–76.
- Mante, J., Gerowitt, B., 2007. Perspektiven für blütenreiche Saumbiotop in intensiv genutzten Agrarlandschaften On perspectives for flowering field boundaries in intensively used agricultural regions. *Gesunde Pflanzen* 59 (2), 71–76.
- Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M., Batáry, P., Garibaldi, L., 2018. Crop rotation and agri-environment schemes determine bumblebee communities via flower resources. *J. Appl. Ecol.* 55 (4), 1714–1724.
- Martins, K.T., Albert, C.H., Lechowicz, M.J., Gonzalez, A., 2018. Complementary crops and landscape features sustain wild bee communities. *Ecol. Appl.* 28 (4), 1093–1105.
- Menz, M.H.M., Phillips, R.D., Winfree, R., Kremen, C., Aizen, M.A., Johnson, S.D., Dixon, K.W., 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends Plant Sci.* 16 (1), 4–12.
- Otto, C.R.V., O'Dell, S., Bryant, R.B., Euliss Jr., N.H., Bush, R.M., Smart, M.D., 2017. Using publicly available data to quantify plant-pollinator interactions and evaluate conservation seeding mixes in the Northern Great Plains. *Environ. Entomol.* 46, 565–578.
- Paini, D.R., 2004. Impact of the introduced honey bee (*Apis mellifera*) (Hymenoptera: Apidae) on native bees: A review. *Austral Ecol.* 29 (4), 399–407.
- Paul, C., Hanley, N., Meyer, S.T., Fürst, C., Weisser, W.W., Knoke, T., 2020. On the functional relationship between biodiversity and economic value. *Sci. Adv.* 6, eaax7712.
- Pe'er, G., Dicks, L.V., Visconti, P., Arlettaz, R., Báldi, A., Benton, T.G., Collins, S., Dieterich, M., Gregory, R.D., Hartig, F., Henle, K., Hobson, P.R., Kleijn, D., Neumann, R.K., Robijns, T., Schmidt, J., Schwartz, A., Sutherland, W.J., Turbé, A., Wulf, F., Scott, A.V., 2014. EU agricultural reform fails on biodiversity. *Science* 344 (6188), 1090–1092.
- Porto, R.G., de Almeida, R.F., Cruz-Neto, O., Tabarelli, M., Viana, B.F., Peres, C.A., Lopes, A.V., 2020. Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Security* 12, 1425–1442.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353.
- Quinlan, G.M., Milbrath, M.O., Otto, C.R.V., Isaacs, R., 2021. Farmland in U.S. Conservation Reserve Program has unique floral composition that promotes bee summer foraging. *Basic Appl. Ecol.* 56, 358–368.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdansk, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11 (5), 499–515.
- Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. *Biol. Conserv.* 141 (2), 417–426.
- Rundlöf, M., Persson, A.S., Smith, H.G., Bommarco, R., 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol. Conserv.* 172, 138–145.
- Rundlöf, M., Lundin, O., Bommarco, R., 2018. Annual flower strips support pollinators and potentially enhance red clover seed yield. *Ecol. Evol.* 8 (16), 7974–7985.



- Runge, T., Latacz-Lohmann, U., Schaller, L., Todorova, K., Daugbjerg, C., Termansen, M., Liira, J., Le Gloux, F., Dupraz, P., Leppanen, J., Fogarasi, J., Vigh, E.Z., Bradfield, T., Hennessy, T., Targetti, S., Viaggi, D., Berzina, I., Schulp, C., Majewski, E., Bouriaud, L., Baci, G., Pecur, M., Prokofieva, I., Velazquez, F.J.B., 2022. Implementation of Eco-schemes in fifteen European Union member states. *EuroChoices* 21 (2), 19–27.
- Sabbahi, R., de Oliveira, D., Marceau, J., 2005. Influence of honey bee (Hymenoptera: Apidae) density on the production of canola (Crucifera: Brassicaceae). *J. Econ. Entomol.* 98, 367–372.
- Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J. H.J., Siepel, H., Kleijn, D., 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *PNAS* 111 (49), 17552–17557.
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., Diamond, S., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *J. Appl. Ecol.* 52 (5), 1165–1175.
- Scheper, J., Reemer, M., van Kats, R., Ozinga, W.A., van der Linden, G.T.J., Schaminée, J. H.J., Siepel, H., Kleijn, D., 2021. Attractiveness of sown wildflower strips to flower-visiting insects depends on seed mixture and establishment success. *Basic Appl. Ecol.* 56, 401–415.
- Sidhu, C.S., Joshi, N.K., 2016. Establishing wildflower pollinator habitats in agricultural farmland to provide multiple ecosystem services. *Front. Plant Sci.* 7.
- Sih, A., Baltus, M.-S., 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. *Ecology* 68, 1679–1690.
- Söber, V., Leps, M., Kaasik, A., Mänd, M., Teder, T., 2020. Forest proximity supports bumblebee species richness and abundance in hemi-boreal agricultural landscape. *Agr. Ecosyst. Environ.* 298, 106961.
- Steffan-Dewenter, I., Kuhn, A., 2003. Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. Lond. B* 270 (1515), 569–575.
- Steffan-Dewenter, I., Thies, C., Tscharnkte, T., 2002. Scale-dependent effects of landscape structure on three pollinator guilds. *Ecology* 83, 1421.
- Su, R., Dai, W., Yang, Y., Wang, X., Gao, R., He, M., Zhao, C., Mu, J., 2022. Introduced honey bees increase host plant abundance but decrease native bumble bee species richness and abundance. *Ecosphere* 13, e4085.
- Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. *Nature* 367 (6461), 363–365.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277 (5330), 1300–1302.
- Timberlake, T.P., Vaughan, I.P., Memmott, J., Requier, F., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *J. Appl. Ecol.* 56 (7), 1585–1596.
- Toivonen, M., Karimaa, A.-E., Herzog, L., Kuussaari, M., 2022. Flies are important pollinators of mass-flowering caraway and respond to landscape and floral factors differently from honeybees. *Agr. Ecosyst. Environ.* 323, 107698.
- Tonietto, R.K., Larkin, D.J., Diamond, S., 2018. Habitat restoration benefits wild bees: A meta-analysis. *J. Appl. Ecol.* 55 (2), 582–590.
- Venjakob, C., Klein, A.-M., Ebeling, A., Tscharnkte, T., Scherber, C., 2016. Plant diversity increases spatio-temporal niche complementarity in plant-pollinator interactions. *Ecol. Evol.* 6 (8), 2249–2261.
- von Königslöw, V., Fornoff, F., Klein, A.-M., 2022. Wild bee communities benefit from temporal complementarity of hedges and flower strips in apple orchards. *J. Appl. Ecol.* 59 (11), 2814–2824.
- Westphal, C., Steffan-Dewenter, I., Tscharnkte, T., 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia* 149 (2), 289–300.
- Wix, N., Reich, M., Schaarschmidt, F., 2019. Butterfly richness and abundance in flower strips and field margins: the role of local habitat quality and landscape context. *Heliyon* 5 (5), e01636.
- Wood, T.J., Holland, J.M., Goulson, D., 2015. Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biol. Conserv.* 187, 120–126.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *PNAS* 96 (4), 1463–1468.