Basic and Applied Ecology

Limited honeybee hive placement balances the trade-off between biodiversity conservation and crop yield of buckwheat cultivation

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Abstract

An increasing number of farmland initiatives aim to aid biodiversity conservation through alternative farming practices such as nature-inclusive farming. However, these approaches frequently lead to trade-offs between biodiversity conservation and crop yield. For example, buckwheat (*Fagopyrum esculentum*) is a melliferous crop that flowers for a long period in the summer when nectar in agricultural areas is generally scarce, and buckwheat cultivation could therefore contribute to wild pollinator conservation. However, honeybees (*Apis mellifera*) are placed to ensure sufficient crop pollination, which potentially increases resource competition with wild pollinators in and around the crop. Here, we have studied this trade-off by surveying pollinators in and around 16 small-scale (∼1 ha) flowering buckwheat fields and we determined the contribution of pollinator density to crop yield in a nature-inclusive farming project. We found that the buckwheat pollinator community was diverse, albeit dominated by honeybees. We found no clear indications of resource competition between honeybees and wild pollinators within the buckwheat fields. Honeybee density in the surroundings was generally low, and increased minimally during honeybee-hive placement. While densities of honeybees decreased non-linearly over the day in buckwheat fields, they did not (temporarily) move into the surroundings of the field, suggesting limited competition for resources with wild pollinators. Crop yield was largely dependent on crop pollinator density, notably of honeybees, and to a lesser extent crop biomass (as a proxy for agricultural management). Our results show that buckwheat cultivation fits well within nature-inclusive farming if some simple precautionary measures are being taken, such as limiting the honeybee-hive densities and placing hives only during the main flowering period. The introduction of buckwheat cultivation into crop rotation could then contribute to fill an important nectar gap in the summer, which potentially boosts wild pollinator populations in the long term.

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Keywords: Crop pollination; Pollinator management; Resource competition; Nature-inclusive farming; Buckwheat *Fagopyrum esculentum*; Biodiversity conservation

Introduction

Agricultural intensification is one of the main drivers of biodiversity decline (Dainese et al., 2019), even though the

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ecosystem services that these species deliver are essential to agricultural production (Kleijn et al., 2019). To break with these intensive practices, an increasing number of initiatives focus on alternative farming systems that aim to enhance biodiversity levels while maintaining a profitable crop yield (Kleijn et al., 2019). Depending on the main aim of the initiative, the initiators need to balance the trade-off between biodiversity benefits and crop yield, where, roughly speaking, more biodiversity conservation usually results in lower external inputs and lower total yields (Kremen et al., 2012). To find this balance, we need to understand how biodiversity-friendly these alternative farming practices are, and -particularly so- if crop yield heavily depends on biodiversity-unfriendly practices.

Three-quarters of our global crops are partially depending on insect pollination for crop yield (Klein et al., 2007), which makes pollinator management an essential part of agricultural management in these crops. A general practice for many insect-pollinated crops is to manage insect pollination by placing domestic honeybee (*Apis mellifera*) hives (Rucker et al., 2012). However, honeybee hive rental can be expensive (Rucker et al., 2012), and honeybees can outcompete wild pollinators for flower resources (Henry & Rodet, 2018), increasing the friction between crop yield and biodiversity conservation. If wild pollinators can replace honeybees' pollination services, this would be an attractive alternative for biodiversity-oriented farming practices, but whether this is possible is not always clear.

A problem associated with honeybee-hive placement is that hive placement does not guarantee that the honeybees actually forage on the associated crop. For example, honeybees placed for apple pollination can be drawn away to nearby oilseed rape fields (Osterman et al., 2021), and subsequently displace wild pollinators within the field (Lindström et al., 2016), or for example to nearby flowering strawberry fields (Bänsch et al., 2020). Also, hives are not always removed after (main) flowering of the crop, which can result in a large spill-over of honeybees into semi-natural habitats, thereby affecting wild pollinators' diets and reducing wild flower seed set (Magrach et al., 2017), and reduce wild pollinator populations (Henry and Rodet, 2018). Whether resource competition also takes place within crops is largely unknown (but see indications in Lindström et al. (2016)), but would be undesirable if the crop is partly grown as a biodiversity conservation measure for wild pollinators too.

In a nature-inclusive farming project in the Netherlands (c.f. Erisman et al., Geertsema and Polman (2017); see methods), buckwheat (*Fagopyrum esculentum*) was chosen as a promising nature-friendly commercial crop because of its long flowering period and rich nectar quantities (Cawoy et al., 2009). Buckwheat was a commonly cultivated crop on relatively poor soils in northwestern Europe, but the cultivation was largely abolished due to the invention of artificial fertiliser. As buckwheat flowers are mainly visited by honeybees (next to wild bees and hoverflies), and produces about 20% of the yield without insect pollination (Bartomeus et al., 2014), hive placement is generally deemed necessary (Björkman, 1995; Cawoy et al., 2009), but this may have undesired side effects on the wild pollinator community. To assess the consequences of hive placement on biodiversity conservation aims, we have evaluated whether (1) honeybee-hive placement had an effect on wild pollinator densities within the crop and (2) in the surroundings of 16 small-scale (∼1 ha) agricultural fields, and (3) what the relative contribution is of honeybees and wild bees to buckwheat crop yield. Because honeybees were placed only during the main flowering period (as a precautionary measure), this allowed for a comparison of the buckwheat crop pollinator community before, during and after honeybee hive placement.

Materials and methods

Study system

The study area Westeresch (∼10 km^2) is located in the north of the Netherlands in the province Groningen, roughly between Vlagtwedde, Onstwedde and Wedde (N53.05, E7.07; Appendix A: Fig. S1). The landscape and land use of the study area is historically built around the groundwater-fed streams, with poor sandy soils in the higher elevations with mainly natural areas, wet (peat) marshlands at the lower elevations used as hayland, and at intermediate elevations common agricultural fields (Dutch: 'essen', German: 'Eschflur') enriched with sod cuttings and animal manure (Spek et al., 2015). However, during the green revolution the traditional small-scale fields were intensified and simplified. The Westeresch (consisting of a few smaller 'essen') is now owned by the State Forestry Service (Staatsbosbeheer), and in 2018 they started a nature-inclusive farming project (definition c.f. Erisman et al. (2017)). They transformed the intensive agricultural fields to small-scale organic agriculture with ample space for biodiversity conservation. The fields are now roughly one hectare large, and have a crop rotation of about six years with different cereals, peas, beans, lupin, grass-clover and buckwheat. Within this project, we selected thirteen organically managed buckwheat fields (not all certified organic) in 2021 that were separated from each other by at least one other crop field (minimum >100 meter) or none if that field contained a different cultivar of buckwheat (Appendix A: Fig. S2). Additionally, we included three (certified) organic buckwheat fields owned by Natuurmonumenten, another nature conservation organization, that were located up to 5 km south of Vlagtwedde (N53.01, E7.12) and further apart from each other (>1.3 km; Appendix A: Fig. S1).

Our focus fields contained three different varieties of common buckwheat (*Fagopyrum esculentum*), mostly containing 'Kora' and 'Drushina', one field of 'Devyatka', and one field of tartary buckwheat (*Fagopyrum tataricum*), which is fairly similar in flower biology to common

buckwheat. Buckwheat has distylous flowers with pin (long pistil, short stamen), and thrum (short pistil, long stamen; fewer and larger pollen, and relatively more nectar) flowers that both produce seeds (Cawoy et al., 2009). Buckwheat starts flowering about 30−40 days after sowing, and can continue to flower until winter, but the main flowering period is about 55−80 days after sowing (Cawoy et al., 2009; Strahm et al., 2019). The flowers that are pollinated in the main flowering period are harvested in the end of August-beginning of September, even though at that time there are still flowers and unripe seeds (Cawoy et al., 2009). Depending on the crop field, buckwheat was sown in rows or broadcasted between May 15th and May 25th 2021.

Pollinator management

Because buckwheat in Europe is mainly visited by honeybees (Bartomeus et al., 2014; Jacquemart et al., 2007; Strahm et al., 2019) honeybee hives were placed next to the fields. A professional biodynamic beekeeper placed on average two hives per hectare, which is at the low end of recommendations (2 to 5 hives per hectare c.f. (Björkman, 1995; Goodman et al., 2001). To increase the variation in honeybee density across all study fields, we varied the actual hive density between none and five hives per hectare. However, as the fields were located close together, honeybees placed at one field could easily visit the other fields. Honeybee hives were placed from July 12th to August 3rd 2021, and covered the main flowering period. Three hives were fitted with a digital scale that measured and stored hive weight on an hourly basis.

Insect monitoring

We used transect walks to monitor (wild) bees and hoverflies in herbaceous semi-natural habitats, and (wild) bees, hoverflies and butterflies in the buckwheat fields (c.f. Fijen et al., Raemakers and Kleijn (2019)), which covers the major groups of flower visitors. Each transect was placed on a fixed location, and consisted of 150 m long and one meter wide transects (i.e., 150 m^2), subdivided in three equal sub-transects of 50 m^2 to spread the search effort evenly over the transects. During each visit, we monitored insect flower visitors for five minutes in each sub-transect, excluding handling time, totalling 15 min per transect. Insects were identified to species level on the wing where possible, and collected and stored for later identification when this was not possible. We considered *Bombus terrestris/lucorum/magnus* as a species complex, as they cannot be identified reliably without genetic analysis (Williams et al., 2012). After each transect visit in the semi-natural habitats, we identified all the flowering species and counted the number of flowers per species to calculate flower cover (based on species-specific measurements of flower size − data not

published). Transects were walked in favourable weather conditions for pollinators (>15 °Celcius, <5bft wind, c.f. Fijen et al., Morra and Kleijn (2021))

A transect in the buckwheat field was located roughly 20 m parallel to the long field edge and started at the short field edge. We aimed to monitor these transects twice during buckwheat flowering but before honeybee hive placement, three times during buckwheat flowering and during honeybee hive placement, and two times during buckwheat flowering and after honeybee hive placement. We selected 13 semi-natural habitat transects in the study area, at varying distances to buckwheat fields (0−1200 m). Transects were located in road/field verges, herbaceous nature areas or in newly created semi-natural patches close to crop fields. We aimed to monitor these transects three times before buckwheat flowering, once during flowering before honeybee hive placement, three times during flowering and during honeybee hive placement, and twice during flowering and after honeybee hive placement. We (randomly) alternated morning and afternoon visits to all transects to cover eventual activity peaks throughout the day.

Crop yield

To determine crop yield, we harvested three randomly selected subplots of 1 m^2 along the pollinator transect in each buckwheat field on August 30th 2021. In each subplot we harvested the full above-ground biomass. We then subsequently dried the bags for three days at 70 °Celsius, weighed the total dry biomass (grams m^2), and threshed the seeds using a mini-combine. We then cleaned the seeds by hand to remove unfertilised seeds, counted the total seeds m^{-2} using a seed counter (Contador, Pfeuffer GmbH) and weighed total seed weight (to 0.1 gram). Dry biomass per subplot (as a measure of field productivity) was then calculated as the total weight minus the harvested seed weight. We used number of seeds m^{-2} and estimated kg ha^{-1} as our crop yield parameters. Two subplots of different fields were excluded due to mistakes in the threshing and cleaning process.

Statistical analyses

To test whether honeybee hive placement had an effect on the wild pollinator community in the buckwheat fields or in the surroundings, we performed three sets of analyses. To test whether the pollinator densities differed with the sampled periods, we first averaged honeybee and wild pollinator densities per period for each transect location. For the semi-natural transects, we additionally averaged the flower cover for each period and transect location. We used linear mixed effects models using the function 'lmer' in the lme4 R package (Bates et al., 2015). Within the buckwheat fields, we tested whether pollinator densities depended on the interaction and main effects of species group (honeybees and wild

pollinators) and period, and included field ID as our random effect. We used a similar approach for the semi-natural habitat transects, except here the densities were log10(+1)-transformed to meet normality of residuals, and we included average flower cover (scaled) as a covariable, and transect ID as our random effect.

A negative relation between honeybee densities and wild pollinator densities could indicate interspecific displacement. We therefore tested whether the density of honeybees during honeybee hive placement was related to the wild pollinator density using simple regressions, separately for buckwheat fields and semi-natural transects.

Because buckwheat nectar supplies are frequently depleted in the afternoon (Lee & Heimpel 2002), and this could temporarily increase honeybee displacement to semi-natural habitats, we also explored whether pollinator abundances differed throughout the day, both in the buckwheat fields (Jacquemart et al., 2007) as in the surroundings. To this end, we used all transect counts during honeybee hive placement, and rounded them to the full hour. We then tested for a linear and a second order polynomial trend of pollinator densities, separately for honeybees and wild pollinators, and separately for buckwheat and semi-natural habitat transects. We used mixed effect models with square-root transformed densities (to meet normality of residuals) as our response, hour of day and I(hour of day^2) as our explanatory variables, and site as our random effect.

To test the relative contribution of honeybees and wild pollinators to the crop yield of buckwheat, we only assessed the buckwheat pollinator transects during the main flowering period, because this period is linked to the harvesting. We first checked whether dry biomass or crop cultivar had an effect on average pollinator densities in the buckwheat fields, but this was not the case (i.e., VIF around 1) and both variables were included. We analysed total seeds m^{-2} and estimated kg ha^{-1} as separate response variables using linear regression, and included average pollinator density (all pollinators, honeybees, or wild pollinators), dry biomass and their interaction as explanatory variables. As the cultivars differed in yield parameters (Aubert et al., 2021), we included cultivar as covariable. Continuous explanatory variables were scaled before these analyses. Initially, we included species richness as well, but because the variation in species richness was low (see results), and effects absent, we excluded this from final models to reduce overparameterization of the models. A model including both honeybees and wild pollinators as separate explanatory variables (to test their relative contribution to crop yield) had too high multicollinearity with biomass (VIF > 5) to be ran in full, and excluding biomass from the model produced models with higher AICc and less variation explained. This model could therefore not be included in the analyses. Because the insect densities and crop yield of one field seemed to be an outlier, we checked whether removing this field from the analyses influenced results. Because the trend of the results did not change, and because the biomass of that field was average, we did not consider this field as an outlier.

All models were checked to meet normality of residuals and homogeneity of variances. Significance of results was assessed using log-likelihood ratio tests. For post-hoc comparisons, we used a Tukey test with the function 'glht' from the package multcomp (Hothorn et al., 2016). All analyses were performed in R version 4.0.2 (R Core Team, 2020).

Results

Within the buckwheat fields, we counted 19.358 insects, of which 49% were honeybees (*Apis mellifera*), 38% hoverflies (Syrphidae; 28 species), 12% wild bees (12 species), and 1% butterflies (13 species), in a total of 122 transects (full species list in Appendix A: Table S1). On average, we found 14.6 species (range: 10−21 species) before honeybee hive placement, 23.1 species (range: 19−26 species) during hive placement, and 20.2 species (range 16−24 species) after hive placement per crop field. Within the semi-natural habitats, we counted 3.285 insects, of which 48% were hoverflies (Syrphidae; 27 species), 46% wild bees (33 species) and 6% honeybees (*Apis mellifera*), in a total of 117 transects. Flower species and their respective covers can be found in Appendix A: Table S2.

Transects in the buckwheat fields were visited on average (mean ± SE) 2.4 ± 0.20 during flowering before hive placement, 3.6 ± 0.13 times during flowering and hive placement, and 2.0 ± 0.0 times during flowering and after hive placement. The SNH-transects were visited on average (mean ± SE) 2.8 ± 0.10 times before flowering, 0.9 ± 0.08 during flowering and before hive placement (all once, except for one transect at 1200 meter from a buckwheat field), 3.1 ± 0.08 times during flowering and hive placement, and 2.15 ± 0.10 times during flowering and after hive placement.

Insect densities within buckwheat fields

The insect densities within the buckwheat fields differed before, during and after honeybee hive placement, and per insect group (i.e., significant interaction period*species group; χ^2 (2) = 25.93, p <0.001; Fig. 1). Honeybee density was higher during honeybee hive placement, but similar before and after hive placement. Wild pollinator densities were two-thirds lower before hive placement than during and after hive placement. Densities of honeybees and wild pollinators did not differ from each other before and during hive placement, but wild pollinators were almost three times as abundant as honeybees after hive placement.

Honeybee densities in the buckwheat fields during honeybee hive placement were not related to the wild pollinator densities ($F_{1,14}$ = 1.93, β = −0.19, p = 0.19; Appendix A: Fig. S3A).
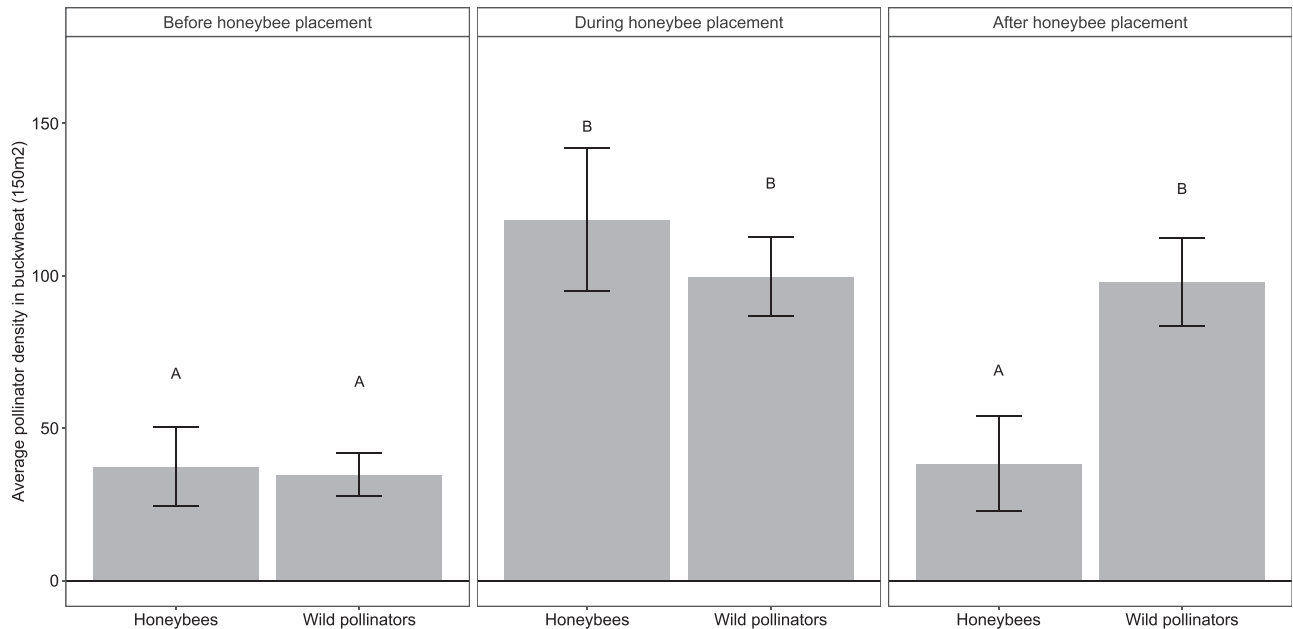
Fig. 1. Average honeybee and wild pollinator densities in buckwheat transects in the sampled periods. Bars show mean values and error bars 95% confidence interval. Letters indicate homogeneous subsets of groups based on the significant interaction between period and species group.

Honeybee densities in the buckwheat fields decreased non-linearly over the day (χ^2 (1) = 5.85, p = 0.02), and most markedly after 12−13 h, while wild pollinator densities decreased linearly over the day (χ^2 (1) = 6.70, p = 0.009; Fig. 2).

Insect densities in semi-natural habitats

The insect densities in the semi-natural habitat transects differed before flowering, and before, during and after honeybee hive placement, and per insect group (i.e., significant interaction period*species group; χ^2 (2) = 10.77, p = 0.01; Fig. 3), and increased with flower cover (χ^2 (1) = 6.43, p = 0.01). Honeybees' density was generally low, but was slightly higher during honeybee hive placement than after hive placement (decreased on average (mean ± SE) from 4.1 ± 1.3 to 2.0 ± 1.51 honeybees per transect), but did not differ from other periods. Wild pollinator densities almost doubled during and after hive placement compared to before flowering and before hive placement. Densities of wild pollinators were always manifold higher than honeybee densities (Fig. 3).

Honeybee densities in the semi-natural habitat transects during honeybee hive placement were not significantly correlated to the wild pollinator densities ($F_{1,11}$ = 3.36, β = 1.66, p = 0.09; Appendix A: Fig. S3B).

Honeybee densities in the semi-natural habitats did not differ throughout the day (χ^2 (1) = 0.17, p = 0.68), nor did the wild pollinator densities (χ^2 (1) = 0.33, p = 0.57; Fig. 2).

Crop yield

The average number of seeds produced per square meter was best explained with a model including all pollinators (Table 1; Fig. 4). The number of produced seeds m^{-2} increased with increasing pollinator density, and with increasing dry biomass (Fig. 4), irrespective of cultivar. When analysed separately, a model including only honeybee or wild pollinator densities showed a positive effect of honeybees, and a marginally non-significant positive effect of wild pollinators (Table 1).

When extrapolating to kg ha^{-1}, we found that a pollinator density increased crop yield, and depended on cultivar (marginally non-significant), and less on dry biomass (Table 1; Fig. 5). When analysed separately, a model including only honeybee or wild pollinator densities showed marginally non-significant positive effects of honeybees, and wild pollinators (Table 1).

Discussion

In this study, we have found that the placement of honeybee hives for buckwheat pollination did not seem to affect wild pollinator densities in the crop, and did not substantially increase honeybee densities in the surroundings. Both honeybees and wild pollinators (both ~50% of all pollinators) contributed to crop yield. These results show that the limited placement of honeybee hives has no strong negative effects on wild pollinators, but is necessary for high crop yields. At the same time, the diverse set of wild pollinators
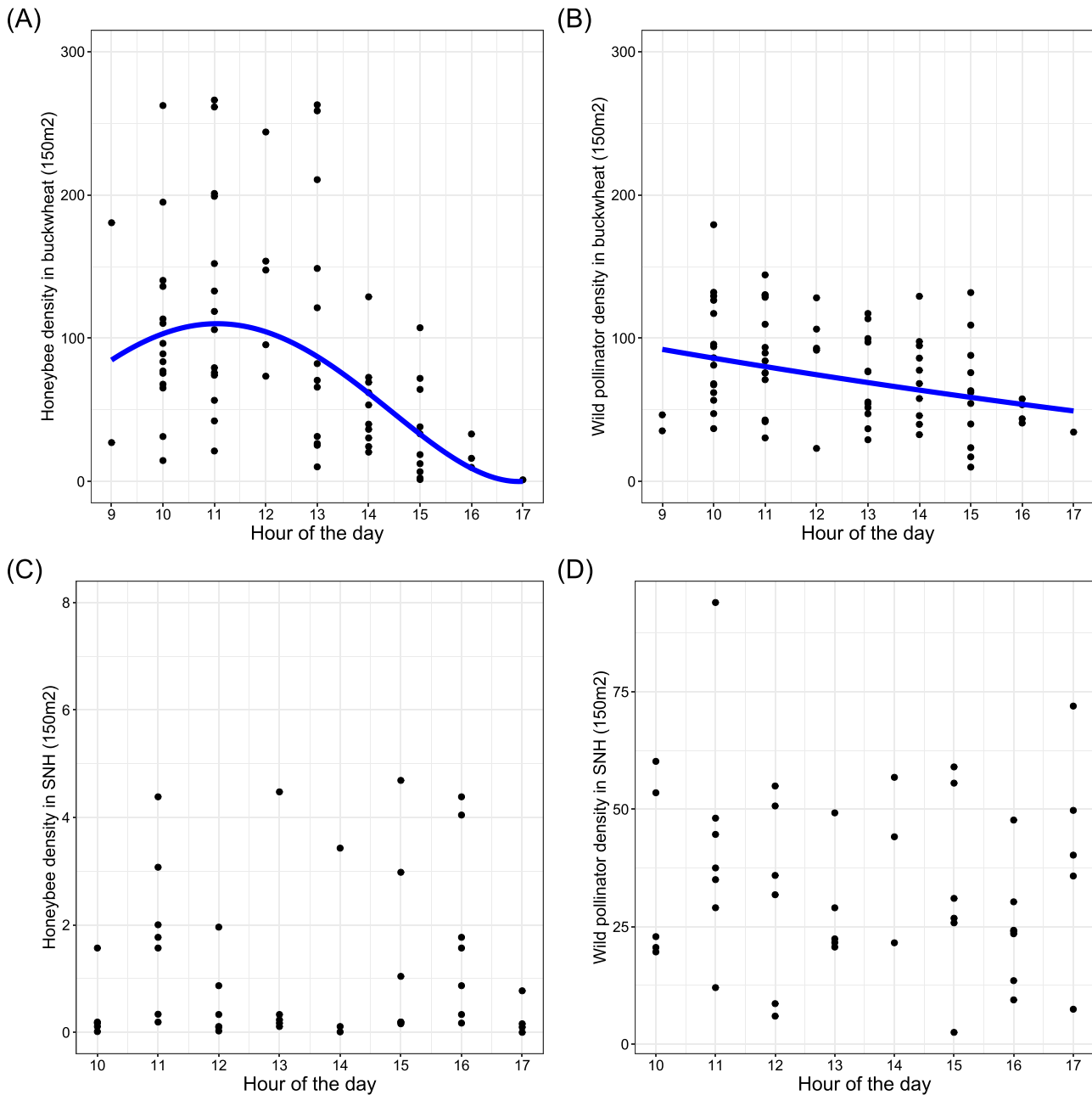
Fig. 2. Average insect densities over the day in and around buckwheat fields during honeybee hive placement. Panel A ($p = 0.02$) and C (n.s.) indicate honeybee densities, while panel B ($p<0.01$) and D (n.s.) indicate wild pollinator densities. Points are back-transformed partial residuals.

will likely benefit from buckwheat cultivation, and therefore buckwheat seems a promising crop to be used as a biodiversity conservation measure.

Wild pollinator densities in the buckwheat fields were equally high during and after honeybee-hive placement, suggesting that there was no resource competition with honeybees within the flowering buckwheat fields. Due to the small study area, we had no effective control fields with few honeybees, which means that we cannot be sure that there was no competition. However, if there was strong competition for resources in these fields, we would have expected to see

an increase of wild pollinators after the hives had been removed, and a negative correlation between honeybee and wild pollinator densities. If resource availability was limited due to honeybee presence, control fields could have revealed higher densities of wild pollinators in the main flowering period. However, such a scenario is not likely as mass-flowering crops (and particularly melliferous crops such as buckwheat) can provide large quantities of resources due to the large cover of high flower density (Schellhorn et al., 2015) compared to the flower resources in the semi-natural habitats in agricultural landscapes (Timberlake et al., 2019). In
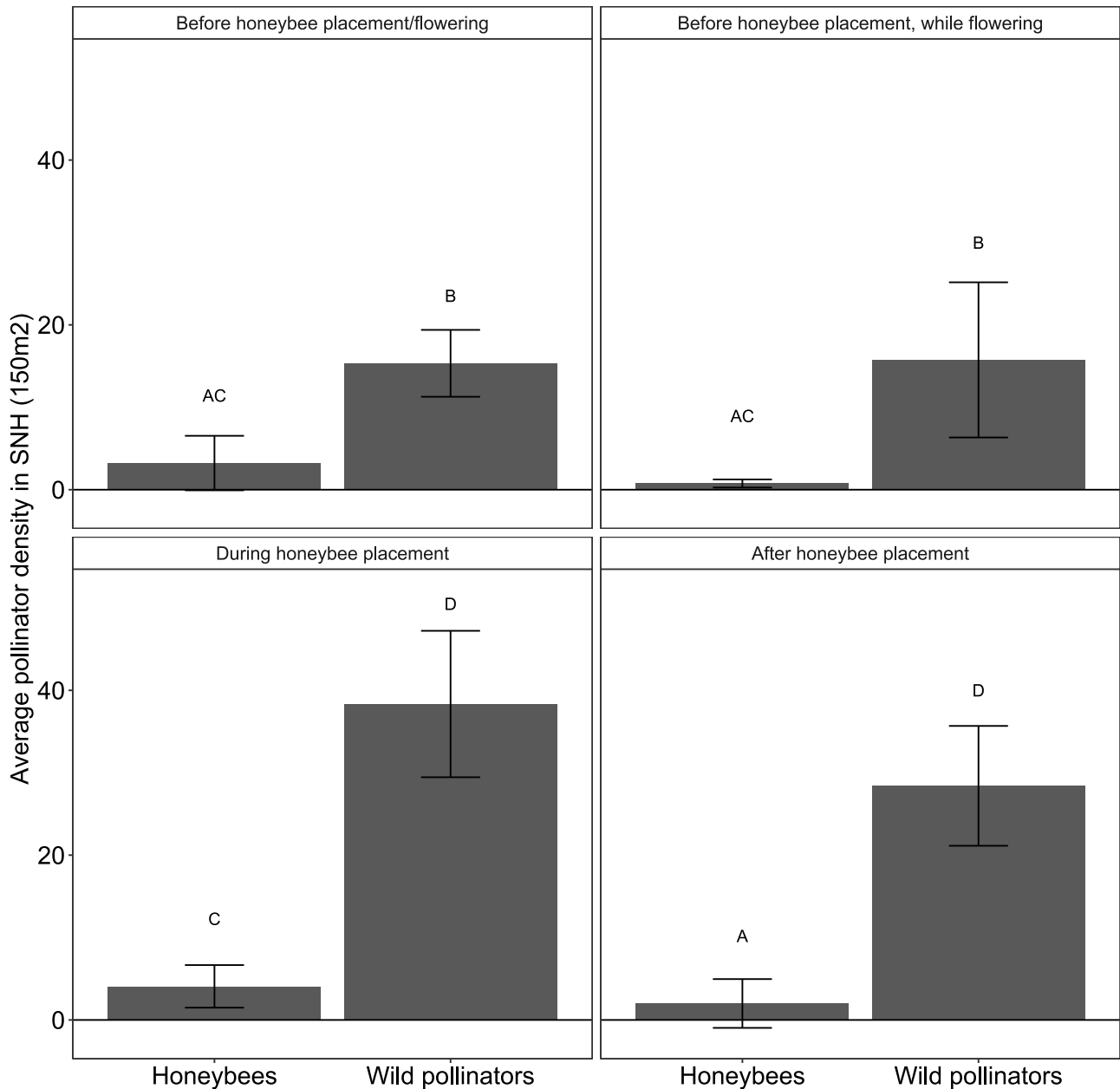
Fig. 3. Average honeybee and wild pollinator densities in semi-natural habitat transects in the different sampling periods. Bars show mean values and error bars 95% confidence intervals. Letters indicate homogeneous subsets of groups based on the significant interaction between period and species group.

oilseed rape, fields with honeybee hives at the crop fields (2 ha^{-1}) and in the surroundings did result in lower densities of wild pollinators (Lindström et al., 2016), although this may (partly) have been a carry-over effect of year-round honeybee hive presence in these landscapes (Bommarco et al., 2021; Henry et al. 2018). As we did not find such indications, it seems unlikely that there was resource competition within the main flowering period of buckwheat.

We also found little influence of honeybee hive placement to the pollinator densities in the surroundings of the buckwheat fields. Overall, honeybee densities were steadily low, suggesting that the diverse flower-rich patches in the surrounding were not so attractive to honeybees. Honeybees preferentially forage on mass-flowering plant species (Seeley, 1995), and avoid the diverse flower patches (Rollin et al., 2013). However, honeybee densities in the buckwheat fields decreased steeply in the afternoon, which begs the question where the honeybees went in the afternoon. Of the mass-flowering crops present in the near surroundings, grass-clover fields (with red clover *Trifolium pratense*) seems a possible candidate (Rundlöf et al., 2018), as the other two flowering crops (common pea *Pisum sativum* and narrow-leaved lupin *Lupinus angustifolius*) crops are hardly visited by honeybees (Fijen et al., 2021; McPhee, 2005).

Table 1. Model estimates for crop yield analyses. Pollinator density is the average density in a 150 m² transect, biomass in grams per m². A '+' sign indicates that this factor was included in the model, but does not have a parameter estimate. P-values < 0.05 are given in **bold**.

	Pollinator density			Biomass			Cultivar			Model		
	Parameter estimate	Chi² (df = 1)	p-value	Parameter estimate	Chi² (df = 1)	p-value	Parameter estimate	Chi² (df = 3)	p-value	AICc	ΔAICc	R²
Seeds/m²												
All pollinators	1085.8	11.85	**0.006**	818.3	5.79	**0.037**	+	1.79	0.212	288.19	0	0.77
Honeybees only	1064.5	6.23	**0.032**	344.7	0.63	0.450	+	1.79	0.212	292.95	4.76	0.68
Wild pollinators only	1454.1	4.59	0.058	1975.5	8.19	**0.017**	+	3.77	**0.048**	294.65	6.46	0.65
Kg/ha												
All pollinators	237.9	8.95	**0.014**	129.8	2.29	0.160	+	3.55	0.056	244.10	0	0.77
Honeybees only	232.2	4.95	0.050	26.4	0.06	0.810	+	2.82	0.093	247.88	3.78	0.70
Wild pollinators only	322.6	3.90	0.076	386.6	5.42	**0.042**	+	6.62	**0.010**	249.05	4.95	0.68

Honeybees may also have been foraging on some abundantly flowering (preferred) species outside our transects, such as bramble (*Rubus fruticosus*), which may cause competition with wild pollinators (Wignall et al., 2020). However, the most likely explanation is that the honeybees returned to their hive as soon as buckwheat nectar was depleted in the afternoon (Lee and Heimpel, 2002), which is known for nectar-collecting honeybees (Meikle et al., 2018). Indeed, the hives fitted with scales indicate that foraging occurred almost exclusively between 9 and 15 h, and almost no bees return thereafter (Appendix A: Fig. S4). Together with the diurnal honeybee density patterns in the buckwheat fields and surroundings, this indicates that honeybees placed for buckwheat pollination also do not outcompete the wild pollinators in the surroundings of the crop field.

Increasing insect densities in buckwheat fields was more important for crop yield than increasing biomass production, showing the importance of insect pollination management compared to other agricultural management practices (Chen et al., 2021; Fijen et al., 2018; Fijen et al., 2020). Due to intercorrelations, the relative contribution of managed honeybees and wild pollinators could not be reliably established, but given that a model with all pollinators explained more variation than models with only honeybees or wild pollinators suggests that both groups contribute to buckwheat pollination (Taki et al., 2010; Taki et al., 2009). About half of all insects present during main flowering were wild pollinators, which was similar to earlier results in Belgium (Jacquemart et al., 2007). Of these, hoverflies were rather abundant in the fields, and the common hoverfly species that we found are fairly efficient pollinators of buckwheat (Liu et al., 2020), underlining the importance of non-bees as crop pollinators (Rader et al., 2016). These results show that buckwheat farmers can also count on wild pollinators' pollination services for high seed yields.

Our results also show the great potential of buckwheat cultivation for biodiversity conservation in agricultural landscapes. Millions of flowers are present during buckwheat flowering, sustaining high densities of wild pollinators with its high nectar resources. For example, at any given moment from the onset of main flowering, the buckwheat fields contained on average about 6500 wild pollinators per hectare. It is quite likely that the populations of these species benefit from this rich addition of resources (Beyer, Gabriel, Kirsch, Schulz−Kesting, Dauber et al. 2020; Riggi et al., 2021), although evidence for increase in hoverfly populations due to mass-flowering crops is largely lacking (Jönsson et al., 2015). Furthermore, buckwheat pollen has relatively low protein contents (14%; Yang et al. (2013)), so pollen-collecting species should obtain their pollen from other (crop) plants, such as from the lupins grown in this study area as well (Fijen et al., 2021). Honeybee hive placement had seemingly little effect on wild pollinators in and around the crop, which justifies the agricultural decision to place a limited number of hives for crop pollination. Interestingly, also without honeybee hives placed, the number of honeybees in
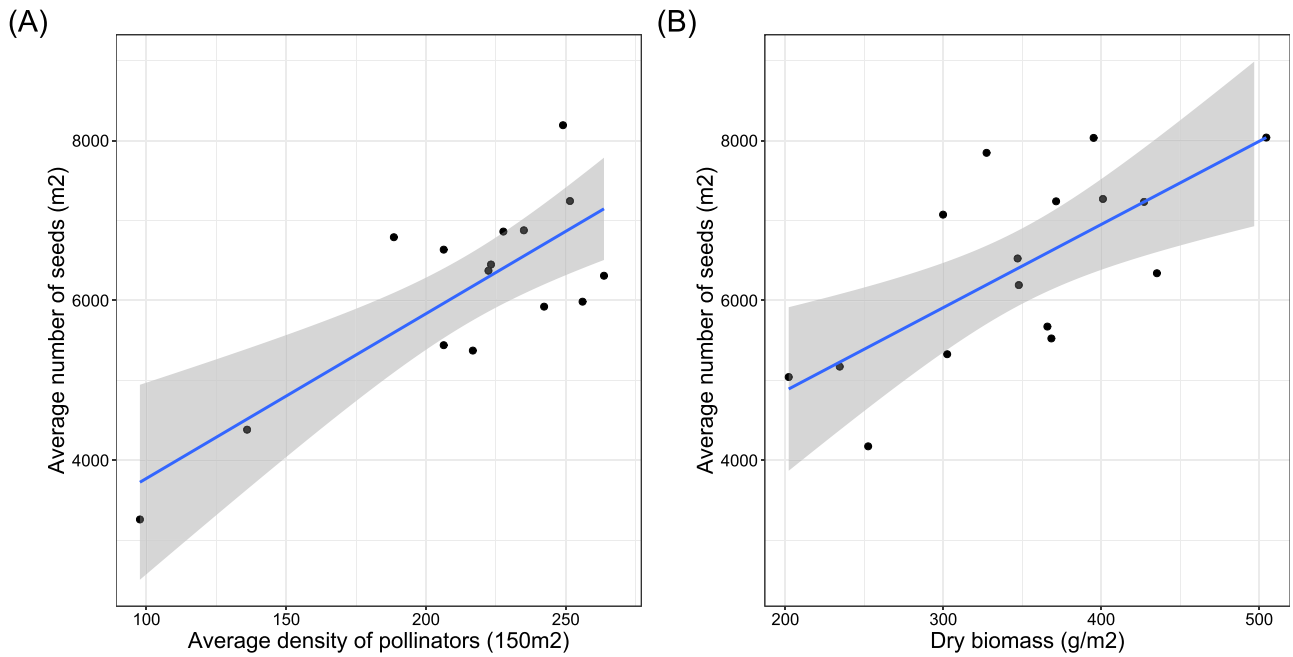
Fig. 4. Buckwheat crop yield (seeds/m^2) in relation to (A) insect density ($p<0.01$) and (B) dry biomass at harvest ($p = 0.04$). Points are back-transformed partial residuals, and gray bands indicate 95% confidence intervals.
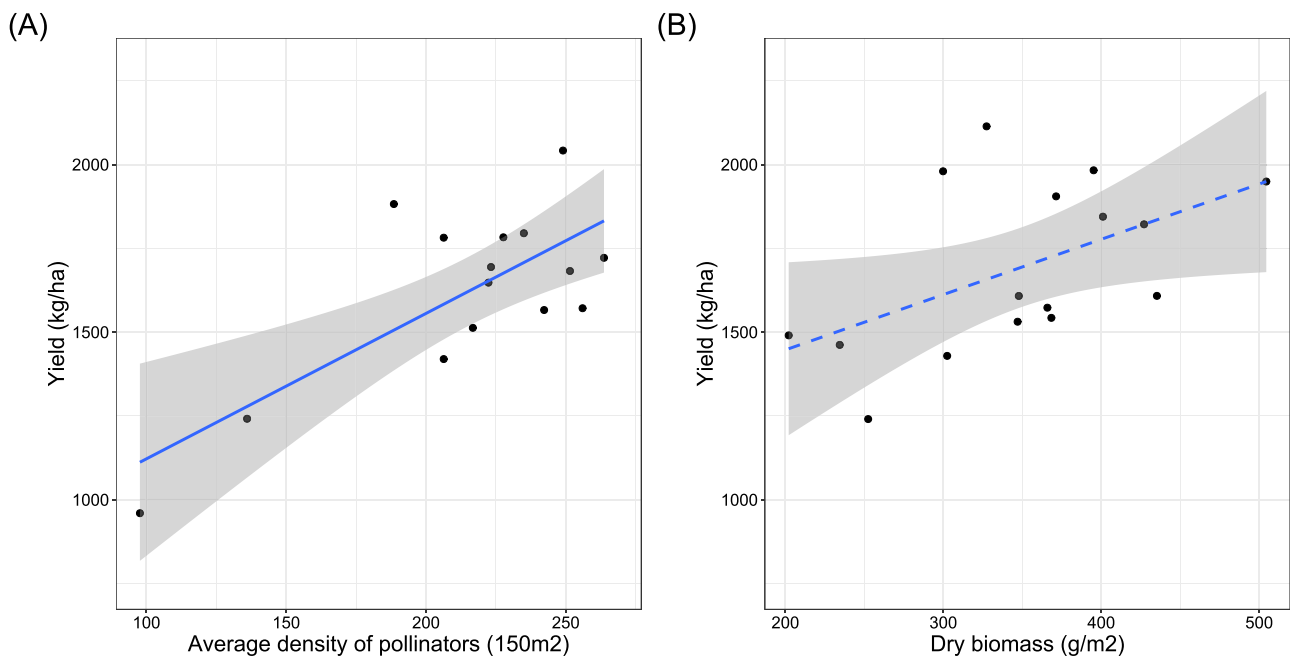

Fig. 5. Estimated buckwheat crop yield (kg/ha) in relation to (A) insect density ($p = 0.01$) and (B) dry biomass ($p = 0.16$) at harvest. Points are back-transformed partial residuals, and gray bands indicate 95% confidence intervals.

the buckwheat fields were substantial (~2600 individuals/ha), showing that the buckwheat fields lure away honeybees from the nearby (semi-)natural habitats. This is a promising result from a biodiversity conservation perspective, as it suggests that buckwheat cultivation can mitigate negative effects of honeybee presence on wild pollinators in semi-natural habitats. However, it remains essential that honeybee hives are only placed during main flowering and in limited densities to avoid conflicts with wild pollinator conservation.

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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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j. baae.2022.09.003.

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