Reduced crop density increases floral resources to pollinators without affecting crop yield in organic and conventional fields

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Abstract

1. Effective weed control in agricultural crop fields increases yields, but simultaneously reduces floral resources for pollinators because many weed species provide pollen and nectar. Consequently, efforts to enhance crop yields on organic farms by using effective weed control methods risk compromising positive effects of organic farming on pollinating insects. Thus, it is important to find management strategies that alleviate the trade-off between crop yields and flowering weeds on organic farms.

2. We investigated the relationship between cereal yields, flowering weeds and bumblebees on organic and conventional arable land. We also investigated the potential of adjusting crop sowing density to benefit flowering weed species richness and floral resources to bumblebees without affecting crop yield.

3. Floral resources and species richness of flowering weeds were higher in organic compared to conventional fields and were negatively related to crop yield in organic but not conventional fields (where the variation of floral resources and flowering weed species richness was comparatively low). Bumblebee species richness was higher in organic compared to conventional fields, and abundance was twice as high in organic as in conventional fields, but not significantly so. Yields in organic fields were two thirds of those in conventional fields. When simultaneously testing the effect of farming type (organic vs. conventional), crop yield and floral resources, only floral resources were related significantly to bumblebee abundance and species richness. A lower sowing density of the crop increased floral resources without negatively affecting crop yield.

4. Synthesis and applications. We show that organic farming practices in cereals benefit bumblebees by allowing more flowering weeds, but at a cost in terms of lower yields. However, adjusting crop sowing density provides an opportunity to attain increased floral resources without negatively affecting crop yields. Thus, by increasing floral resources, adjusting crop sowing density may contribute to supporting high bumblebee densities, which in turn sustain pollination services to wild plants and insect-pollinated crops, such as oilseed rape and field beans, in
agricultural landscapes. We suggest that sowing strategies have the potential to contribute to ecological intensification by supporting organisms that provide ecosystem services to agriculture.

**KEYWORDS**
bumblebees, crop sowing density, ecological intensification, ecosystem services, floral resources, organic farming, pollination, weeds

## 1 | INTRODUCTION

The widespread decline in bees in arable landscapes over the last decades (IPBES, 2016) is of concern given their importance for pollinating cultivated and wild plants (Klein et al., 2006; Ollerton et al., 2011). These declines include bumblebees (Bombus), which are particularly important pollinators in temperate climates (Ollerton, 2017). The abandonment and conversion of natural and semi-natural flower-rich habitats, combined with increasingly effective weed control, has led to a drastic decline in floral resources and diversity in agricultural landscapes (Oerke, 2006; Richner et al., 2015), with concomitant effects on bumblebees (Bretagnolle & Gaba, 2015; Goulson et al., 2015). However, agri-environmental schemes may have resulted in some recovery of floral resources and pollinator communities during later years (Richner et al., 2015; Underwood et al., 2017).

Organic farm management, which is commonly supported and encouraged by agri-environmental schemes, is known to benefit pollinating insects (Tuck et al., 2014). This may not only be related to synthetic insecticides being prohibited (cf. Rundlöf et al., 2015), but also to a generally less intensive management without mineral fertilizers and herbicides that results in increased abundance of flowering weeds both in uncultivated field margins (Henriksen & Langer, 2013) and crop fields (Carrié et al., 2018; Holzschuh et al., 2007). However, because organic farming in general results in lower crop yields compared to conventional farming (Seufert et al., 2012), there is an interest in developing and implementing organic management that enhances crop yields (Röös et al., 2018). Measures to increase yields on organic farms, including exogenous fertilizers and efficient weed management may in turn compromise the biodiversity benefits of organic farming (Flohr et al., 2011; Röös et al., 2018). The pollinator benefit of organic farming from increased floral resources has therefore been suggested to be related to crop yield, such that farming practices that conventionalize organic farming incidentally may result in a loss of its benefits to pollinators (Gabriel et al., 2013).

A potential way to reduce trade-offs between crop yield and biodiversity is to adjust crop sowing density. Crop sowing density is usually adjusted by changing distances between sown seeds to increase the competitiveness of crop plants over weeds (Kolb et al., 2012). In cereal fields, the standard interval for sowing distance between rows (c. 12.5 cm) typically results in higher crop yield and lower weed density compared to wider spacing, such as 25 and 50 cm (Boström et al., 2012; De Vita et al., 2017; Kolb et al., 2012). Also, smaller within-row sowing distances (determined by the amount of seed used) typically increase the crop yield in fields sown with large row intervals, but not in fields sown with the standard row interval (Boström et al., 2012; Kolb et al., 2012). The latter may be because too high sowing densities results in poorer crop grain growth because of increasing intra-crop competition for sunlight and nutrients (Hussain et al., 2003; Weiner et al., 2010). Because of the opposing relationship between high crop density and grain growth, slight differences in sowing distances may not affect crop yields in cereal fields sown with the standard row interval (Weiner et al., 2010). Meanwhile, any decrease in crop sowing density benefits flowering weeds, because of decreased competition early in the growing season when crops are still less affected by intra-crop competition (Weiner et al., 2010). While high weed density is generally negative for crop yields (Oerke, 2006), a certain amount of weeds can exist in crops without substantial yield losses (Adeux et al., 2019), such that total weed suppression may not be necessary to achieve high crop yields (cf. Gaba et al., 2016). Thus, adjusting sowing distances within a certain range provides a potential opportunity to benefit flowering weeds and thereby flower-visiting insects such as bumblebees, without affecting crop yield. The adjustments of crop sowing density would likely have the largest potential to benefit flowering weeds if herbicides are not used, such as in organic systems (Kristensen et al., 2008). In addition to generating benefits to biodiversity, larger sowing distances could result in lower costs to the farmer by reducing the amount of seed sown per field.

In this study, we investigated if conventionalization of organic farming may reduce biodiversity benefits by analysing how floral resources and species richness of flowering weeds are associated with crop yield, as well as how bumblebee abundance and species richness are associated with crop yield and floral resources, in organic and conventional cereal fields. We also analysed if different distances between crop plants within rows and between rows is a potential mechanism to benefit floral resources and species richness of flowering weeds while not affecting crop yield. We hypothesized that floral resources and species richness of flowering weeds would be negatively associated with increasing crop yield, particularly in organic fields because of stronger direct competition between weeds and crops in the absence of herbicide application. Furthermore, we expected bumblebee abundance and species richness to be positively related to increasing floral resources, and that any potential association between bumblebees and crop yield would rather be explained by the correlation between floral resources and crop yield. We also expected that lower realised crop sowing density, through
wider distances between sown seeds within rows, as well as between rows sown with the standard interval (c. 12.5 cm, and additional variance caused by varying conditions when sowing) would result in more flowering weed species and floral resources due to less competition from crops, potentially without compromising crop yield (Kolb et al., 2012).

2 | MATERIALS AND METHODS

2.1 | Study design

The study was conducted on organic and conventional farms in southern Sweden (Figure 1), a region characterized by agricultural land use and temperate climate. We created a study system with 19 farms with two cereal fields each, resulting in a total sample size of 38 cereal fields (Figure 1). Ten of the farms were organic (20 fields) and nine were conventional (18 fields). Both the organic and conventional cereal fields were predominantly sown with barley, but also wheat (six organic and three conventional fields) and oat (one organic and one conventional field). To ensure similar landscape context between the two farming types, we selected both organic and conventional farms along a gradient of semi-natural grasslands in the surrounding landscape. We calculated the proportion semi-natural grassland within a 1-km radius around each focal field (%SNG), which is a radius where landscape context normally affects bees (Steffan-Dewenter et al., 2001), using the Integrated Administration and Control System (IACS) database administered by the Swedish Board of Agriculture, with QGIS version 2.16 (www.qgis.org). We later used %SNG (range 1%–18%) as a control variable when analysing how other predictors related to biodiversity. This enabled us to control that relationships between biodiversity and other predictors were not driven by potential underlying correlations with landscape complexity (Birkhofer et al., 2018; Persson et al., 2010).

2.2 | Data collection

To increase our chances of observing bumblebee and flowering weed species that are active/in bloom during different periods of the growing season, we surveyed bumblebees and flowering weeds five times between 18 May 2017 and 24 August 2017. We surveyed fields along a 1 × 100 m transect within the central parts of the fields. We placed the transects, so that the transect walk would intersect flower-rich parts of the fields, which potentially introduced a bias in abundance estimates compared to actual total field densities. However, this sampling strategy is still likely to reflect the abundance of both flowering weeds and bumblebees similarly among all sampled fields. We estimated floral resources for pollinators based on the percentage of ground surface area that was covered by flower corollas (flower cover) in the transects: <2%, 2%–6%, 6%–10%, 10%–20%, 20%–25% or >25% (e.g. Carrié et al., 2018; Holzschuh et al., 2016). We also recorded the flowering weed species in the transect. Using a modified Pollard walk procedure (Pollard, 1977), we surveyed bumblebees by walking along the same transect for 10 min while recording individuals and species within 1 m on each side of the transect. When possible, we netted and identified individuals to species level in the fields using field keys. We distinguished all netted individuals to species level except that Bombus lucorum (s.l.) and B. terrestris were treated as a single species due to the difficulty of distinguishing them. Individuals that could not be identified to the species level were included in the estimates of abundance but not species richness.

We also visited each field once in the last week of June to collect the measures of realised crop sowing distances to investigate their association with flower cover, flowering weed species richness and crop yield. We surveyed crop sowing distances along a 100-m-long transect (different from the flowering weed and bumblebee survey transect) placed randomly within the central parts of the fields. We placed a 0.5 × 0.5 m frame above the crop plants at five points along each transect. Within the frame, we measured the distance between crop plants within the same row (sowing distance within rows) and between crop plants in different rows (sowing distance between rows; Figure 2).

We obtained crop yield information for each field (estimated as kg/ha for the entire field) from farmers at the end of the season.

2.3 | Statistical analyses

To facilitate statistical analyses, we summed bumblebee abundance; calculated total number of observed flowering weed and bumblebee species; and averaged flower cover as well as sowing distance within...
fields when accounting for flower cover. Therefore, we expanded the GLMMs with bumblebee abundance and species richness as response variables by adding the predictor flower cover and its interaction with farming type. Any non-significant interaction was removed, after which the model was rerun.

In models where we included crop yield as a predictor, we did not necessarily assume that crop yield per se would have a causal effect on flowering weeds or bumblebees, but used it as a proxy variable for yield-enhancing management that we did not measure, for example, use of fertilizers and pesticides (cf. Gabriel et al., 2013; Robinson & Sutherland, 2002).

Finally, we investigated how flower cover, flowering weed species richness and crop yield were related to sowing distances. For these analyses, we excluded four organically managed fields, which were sown with double row spacing (25 cm), instead of the standard (c. 12.5 cm, however in practice there is some additional variation caused by variance in row spacing due to, for instance, slight variations in soil topography). We did this because we wanted to capture the effects caused by variation in sowing density, and not the effect of inter-row hoeing which is typical for double row spacing (Jordbruksverket, 2012). Before modelling the response variables against sowing distances, we checked that sowing distance within rows and between rows was not correlated in the data subset (Pearson’s correlation coefficient = 0.05). We then used GLMMs to analyse how flower cover and flowering weed species richness were related to sowing distance within rows, sowing distance between rows, farming type and its interaction with each of the two sowing distance measures. We used a LMM to analyse how crop yield related to the same set of predictors and interactions, after visually verifying that the model’s residuals were normally distributed and homoskedastic. As above, the models were rerun without potential non-significant interactions.

All of our models included the predictors %SNG and cereal type to control for their potential influence on the response variables. All final LMMs were fitted with restricted maximum likelihood and the GLMMs with maximum likelihood. In the GLMMs, we used different error distributions and link functions depending on the response variables as described below. For flower cover, we assumed a beta error distribution using a logit link function. To use the beta error distribution, we first transformed the flower cover proportions to a zero mean and unit standard deviation. We derived P-values against sowing distances, we checked that sowing distance within rows and between rows was not correlated in the data subset (Pearson’s correlation coefficient = 0.05). We then used GLMMs to analyse how flower cover and flowering weed species richness were related to sowing distance within rows, sowing distance between rows, farming type and its interaction with each of the two sowing distance measures. We used a LMM to analyse how crop yield related to the same set of predictors and interactions, after visually verifying that the model’s residuals were normally distributed and homoskedastic. As above, the models were rerun without potential non-significant interactions.

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for the parameter estimates of the predictors with likelihood-ratio tests. We fitted the models with the R packages glmmTMB (Brooks et al., 2017) and lme4 (Bates et al., 2015), using R version 4.0.0 (www.r-project.org).

3 | RESULTS

3.1 | Differences between organic and conventional fields

Flower cover was higher in organic (12.6 ± 7%, mean ± SD) compared to conventional fields (3.6 ± 3%; χ² = 15.49, p < 0.001). We found 48 flowering weed species (Table S1 in Supporting Information), with more species in organic (7.6 ± 2.8 species, mean ± SD) than in conventional fields (2.8 ± 2.1 species; χ² = 13.84, p < 0.001). Neither flower cover nor flowering weed species richness was related to %SNG (χ² = 1.44, p = 0.23; and χ² = 0.19, p = 0.663) or differed among cereal types (χ² = 0.65, p = 0.724; and χ² = 1.98, p = 0.371).

We found 497 bumblebee individuals belonging to eight species among all samples (Table S2). Bumblebee species richness was higher in organic (3.15 ± 1.3 species) than in conventional fields (2.1 ± 0.8 species; χ² = 6.54, p = 0.011), but their abundance did not differ significantly between farming types (17.4 ± 16.1 individuals in organic and 8.3 ± 6 in conventional fields, χ² = 2.14, p = 0.144).

Neither bumblebee abundance nor species richness was related to %SNG (χ² = 3.56, p = 0.059; and χ² = 0.84, p = 0.359) or differed among cereal types (χ² = 1.68, p = 0.432; and χ² = 1.42, p = 0.492).

Crop yields (normalized across cereal types) were on average 36% lower in organic (3.5 ± 1.3 tonnes/ha) compared to that in conventional fields (5.5 ± 1.5 tonnes/ha; χ² = 8.18, p = 0.012). Crop yields differed among cereal types (χ² = 70.10, p < 0.001) but were not related to %SNG (χ² = 0.01, p = 0.932).

Organic and conventional fields, excluding the four fields where a different sowing technique had been used (see above), had similar sowing distance within rows (organic = 7.3 ± 1.5 cm, conventional = 7.2 ± 1.1 cm) as well as sowing distance between rows (organic = 11.1 ± 0.8, conventional = 10.9 ± 1.4).

3.2 | Relationships between flowering weeds and crop yield

The relation of both flower cover and flowering weeds species richness to crop yield depended on farming type (χ² = 7.81, p = 0.005; and χ² = 10.63, p = 0.001), because of a stronger decrease with increasing crop yield in organic than in conventional fields. Thus, flower cover and flowering weed species richness were higher in organic fields when yields ranged from c. 1.5 to 5 tonnes/ha, and similar to conventional fields beyond 5 tonnes/ha (Figure 3a,b). Flower cover, but not flowering weed species richness, was positively related to %SNG (χ² < 4.41, p = 0.036; and χ² = 2.67, p = 0.102), whereas neither differed among cereal types (χ² = 3.65, p = 0.162; and χ² = 4.70, p = 0.095). Regression coefficients and standard errors are presented in Table S3.

3.3 | Relationships between bumblebees, flowering weeds and crop yield

When not accounting for flower cover, the relation of bumblebee abundance but not species richness to crop yield was dependent on farming type, such that bumblebee abundance decreased more strongly with increasing yields in organic than in conventional fields (χ² = 4.38, p = 0.036, Figure S1a; and χ² = 1.31, p = 0.252). After removing the non-significant interaction term, bumblebee species richness was neither related to farming type (χ² = 1.57, p = 0.210) nor to crop yield (χ² = 3.00, p = 0.083, Figure S1b). Neither bumblebee abundance nor species richness was related to %SNG (χ² = 3.47, p = 0.062; and χ² = 1.32, p = 0.251) or differed among cereal types (χ² = 0.07, p = 0.968; and χ² = 0.58, p = 0.748). Regression coefficients and standard errors are presented in Table S3.
When accounting for flower cover, neither the relation of bumblebee abundance nor species richness to crop yield depended on farming type ($\chi^2 = 1.79, p = 0.181$; and $\chi^2 < 0.01, p = 0.971$). Neither did the relation of bumblebee abundance nor species richness to flower cover depend on farming type ($\chi^2 = 0.69, p = 0.407$; and $\chi^2 = 0.49, p = 0.484$). After removing the non-significant interaction terms, both bumblebee abundance and species richness increased with flower cover ($\chi^2 = 7.05, p = 0.008$, Figure 4a; and $\chi^2 = 4.04, p = 0.044$, Figure 4c), but were not related to farming type ($\chi^2 = 0.2, p = 0.655$; and $\chi^2 = 0.26, p = 0.609$) or crop yield ($\chi^2 = 0.50, p = 0.480$, Figure 4b; and $\chi^2 = 0.43, p = 0.510$, Figure 4d). Finally, bumblebee abundance, but not species richness, was negatively related to %SNG ($\chi^2 = 5.78, p = 0.016$; and $\chi^2 = 1.96, p = 0.161$), but neither differed among cereal types ($\chi^2 = 0.52, p = 0.773$; and $\chi^2 = 0.76, p = 0.684$). Regression coefficients and standard errors are presented in Table S4.

3.4 Relationships between flowering weeds, crop yield and crop sowing distances

When analysing data from fields with standard sowing distances, neither the relation of flower cover nor flowering weed species richness to sowing distance within rows or between rows depended on farming type (cover: $\chi^2 = 0.07, p = 0.789$; and $\chi^2 = 0.77, p = 0.380$; richness: $\chi^2 = 0.77, p = 0.380$; and $\chi^2 = 0.08, p = 0.773$). After removing the non-significant interaction terms, both flower cover and flowering weed species richness were related to farming type ($\chi^2 = 16.10, p < 0.001$; and $\chi^2 = 12.30, p < 0.001$), with higher flower cover and species richness in organic fields. Flower cover and flowering weed species richness increased with increasing sowing distance within rows ($\chi^2 = 6.64, p = 0.010$, Figure 5a; and $\chi^2 = 11.76, p < 0.001$, Figure 5c), but were not related to sowing distance between rows ($\chi^2 = 2.18, p = 0.140$, Figure 5b; and $\chi^2 = 1.15, p = 0.283$, Figure 5d). Flowering weed species richness, but not flower cover, differed among cereal types ($\chi^2 = 7.78, p = 0.020$; and $\chi^2 = 0.30, p = 0.299$). Finally, neither flower cover nor flowering weed species richness was related to %SNG ($\chi^2 = 0.24, p = 0.622$; and $\chi^2 = 0.11, p = 0.736$).
The relations between crop yield and sowing distance within rows and between rows did not depend on farming type ($\chi^2 = 0.21$, $p = 0.659$; and $\chi^2 = 0.21$, $p = 0.654$). After removing the non-significant interaction terms, crop yield was related to farming type ($\chi^2 = 5.90$, $p = 0.030$), with higher crop yields in conventional fields, differed among cereal types ($\chi^2 = 56.57$, $p < 0.001$), but was not related to sowing distance within rows ($\chi^2 = 2.68$, $p = 0.126$, Figure 5e), sowing distance between rows ($\chi^2 = 0.46$, $p = 0.511$, Figure 5f) or to %SNG ($\chi^2 < 0.01$, $p = 0.990$). Regression coefficients and standard errors are presented in Table S5.

4 | DISCUSSION

We show that organic cereal fields harbour more floral resources (measured as flower cover) and richer communities of flowering weeds and bumblebees compared to conventional cereal fields. This demonstrates that organic cereal fields can contribute to the wild plant and pollinator conservation in agricultural landscapes and is in line with previous studies (Bengtsson et al., 2005; Tuck et al., 2014). However, the benefits of organic compared to conventional farming for flowering weeds were mainly apparent when organic crop yields were low. Our results also suggest that higher bumblebee abundance and species richness on organic fields were driven by floral resources.

The lower productivity of organic compared to conventional cereals, as shown in this study and before (Seufert et al., 2012), is usually attributed to higher pathogen attack rates, insufficient weed control and higher nutrient limitation (Seufert et al., 2012). Accordingly, strategies to enhance productivity of organic farming typically involve controlling pathogens and weeds, and adding crop nutrients (Röös et al., 2018). In addition to strategies that aim to control weeds, weeds can be negatively affected by increasing crop yields per se because of increased competition for light, water and nutrients (Gaba et al., 2017).

While our study did not allow for analysing the causal relationship between yield-enhancing management and decreasing plant density and diversity, the negative correlations between organic crop yield and floral resources, as well as species richness of flowering weeds, are consistent with that such yield-enhancing management practices had a negative impact on flowering weeds in organic fields. The absence of an association between crop yield and flowering weeds in conventional fields may be due to weed suppression by herbicides.

The negative correlation between flowering weeds and crop yield in organic fields may not only be caused by yield-enhancing management, but also by the negative impact that high densities of flowering weeds can have on crop yield (Oerke, 2006). However, in comparable systems, crop yield has been interpreted as a proxy for yield-enhancing management (Gabriel et al., 2013; Robinson & Sutherland, 2002), and thus it is likely that a low occurrence of flowering weeds in our system did not reflect a naturally lower occurrence of flowering weeds, but rather more effective weed suppression to enhance crop yields.

Bumblebees collect pollen and nectar from flowering weeds, and thus the beneficial effect that floral resources in cereal fields had on bumblebees in our study was expected (Geppert et al., 2020). Research has shown that bumblebee abundance and species richness in cereal fields correlate negatively with crop yield (Gabriel et al., 2013). We found similar effects of crop yield on organic farms if the effect of floral resources was omitted, but when accounting for both floral resources and crop yield, only floral resources were significantly associated with bumblebees. This indicates that any negative effects of yield-enhancing management were mainly driven by variation in floral resources, which has important implications for maintaining diverse pollinator assemblages in agricultural landscapes. Bumblebees are more mobile than most solitary bees and may be better at finding and utilizing isolated resources in arable fields (Zurbuchen et al., 2010). Thus, other pollinator groups need to be studied to better understand the potential of floral resources in cereal fields to benefit pollinator communities in a broader sense (Powney et al., 2019).

Notably, using a subset of our data that excluded the use of double row spacing, we demonstrated that it is possible to adjust sowing distances to increase the flowering weed species richness and floral resources from weeds without adversely affecting crop yield. Studies that have found higher sowing density to increase crop yield and decrease weed density have typically compared different sowing distances between rows that represented set intervals with relatively large differences (Boström et al., 2012; De Vita et al., 2017; Kolb et al., 2012). When we compared fields sown with the standard sowing distance in Sweden (c. 12.5 cm), an increase in sowing distance within rows from 5 to 10 cm was associated with a twofold increase in floral resources in cereal fields, and an even larger increase in flowering weed species richness (Figure 5a,c; Table S5). The positive relationship between flowering weeds and an increased sowing distance within rows is likely explained by less competition from crops within the crop rows. In contrast, flowering weeds were not related to sowing distance between rows, which may be due to the use of weed harrowing, which targets the spaces between crop rows, and that sowing distance between rows had a comparatively low variation and is affected by local topography. The lack of a response in crop yield from varying sowing distances may be a result of intra-crop compensation, that is, an increased grain weight and/or tiller capacity (Weiner et al., 2010). Thus, our results suggest that within a certain range, adjusting sowing distance within rows (by using fewer seeds) can be a potential strategy to benefit floral resources in arable fields without affecting crop yield. Increasing floral resources by increasing sowing distance within rows could also benefit bumblebees and other pollinating insects in agricultural landscapes. Although there is a rich literature on how adjustments of sowing distances affect crop yields, its impact on biodiversity, other than weed density, has largely been ignored. Flowering weeds in crop fields can play an important role in supplying sufficient floral resources to maintain viable pollinator communities and pollination services to insect-pollinated crops and wild plants in agricultural
landscapes (Bretagnolle & Gaba, 2015). We call for further experimental studies on the effects of adjusting sowing distances, to control for bias if farmers are adapting sowing density to local conditions and to evaluate its full ecological and economic potential as a management strategy to benefit biodiversity.

Although cereal type and %SNG were principally included as control variables (cf. Seufert et al., 2012; Tuck et al., 2014), they were significantly related to response variables per se. Crop yield differed among cereal types (despite being normalized across cereal types), possibly because farmers adjust their crop choice to local conditions. Cereal fields can be undersown with ley, whereas for barley where we had sufficient data, we found no evidence that fields followed by leys differed in crop yields, nor in flower cover, flowering weed species richness, bumblebee abundance or bumblebee species richness (Table S6). We found that an increasing %SNG was associated with increasing floral resources and, surprisingly, decreasing bumblebee abundances. Semi-natural grasslands can benefit plant dispersal to arable fields by increased cross-habitat spill over, which may explain why floral resources increased with %SNG (cf. Roschewitz et al., 2005). Regarding bumblebees, it is possible that they disproportionally foraged in semi-natural grasslands when these comprised a larger proportion of the landscape (Carrié et al., 2018).

In summary, organic farming is widely used as a strategy to mitigate the negative effects from agricultural production on biodiversity. Given the ongoing tendency to increase crop yield on organic farms (cf. Schrama et al., 2018), it is increasingly important to develop strategies to retain the positive effects of organic farming on biodiversity. Indeed, the decreased amount of floral resources and flowering weed species richness in high-yielding organic fields in our study suggested that yield-enhancing management have negative consequences for flowering weeds and taxonomic groups that forage on them, such as bumblebees. Importantly, we showed that decreased sowing density can contribute to maintaining benefits from organic farming to flowering weeds and the resources they provide to pollinator communities in agricultural landscapes, without having negative effects on crop yield. More precisely, our results suggest that sowing distance within crop rows could be increased from 5 to 10 cm without yield losses, while simultaneously leading to decreased seed costs and benefits to flowering weeds.

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Authors’ Contributions

W.S.-H., H.G.S., J.E. and S.A.M.L. conceived the ideas and designed the methodology; W.S.-H., R.C. and J.E. collected the data; W.S.-H. analysed the data with input from H.G.S. and J.E.; W.S.-H. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.mOcfxp3k (Sidemo-Holm et al., 2021).

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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