

Natural and within-farmland biodiversity enhances crop productivity

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Abstract

Ongoing expansion of large-scale agriculture critically threatens natural habitats and the pollination services they offer. Creating patches with high plant diversity within farmland is commonly suggested as a measure to benefit pollinators. However, farmers rarely adopt such practice, instead removing naturally occurring plants (weeds). By combining pollinator exclusion experiments with analysis of honeybee behaviour and flower-visitation webs, we found that the presence of weeds allowed pollinators to persist within sunflower fields, maximizing the benefits of the remaining patches of natural habitat to productivity of this large-scale crop. Weed diversity increased flower visitor diversity, hence ameliorating the measured negative effects of isolation from natural habitat. Although honeybees were the most abundant visitors, diversity of flower visitors enhanced honeybee movement, being the main factor influencing productivity. Conservation of natural patches combined with promoting flowering plants within crops can maximize productivity and, therefore, reduce the need for cropland expansion, contributing towards sustainable agriculture.

Key words: crop pollination limitation, ecosystem services resilience, food security, *Apis mellifera* L., trade-offs, flower-visitation networks, food web.

Introduction

Pollinator-dependent crops are increasingly becoming an important component of human diets (Klein *et al.* 2007; Aizen *et al.* 2008), with their area of cultivation greatly increasing worldwide over the past 50 years (*e.g.* sunflowers increased by 375%, see FAO 2010). Studies done within areas that use the same farming practices and cultivar reveal that, by isolating crop-fields from the pollinator diversity that natural habitat harbours, the expansion of agriculture is leading to negative effects on yields of pollinator dependent crops (*e.g.* Kremen *et al.* 2002; Carvalheiro *et al.* 2010).

Advice to farmers about maintaining and restoring pollinator communities commonly involves the creation of areas rich in plant diversity within farming landscapes (*e.g.* Keitt 2009; Holzschuh *et al.* 2010). However, such measures are seldom adopted by farmers, possibly because of costs inherent in applying such practices, such as the loss of arable land (Ghazoul 2007), or fear of competition for resources between wild plants and the crop (Weiss 1983). In fact, the opposite is more frequent, with wild occurring plants (commonly known as weeds) being exhaustively removed from extensive cultivation fields (Weiss 1983). If farmers are to adopt measures that benefit biodiversity, it is vital to assess benefits and costs of the methods suggested to enhance plant diversity within farmland. Any attempt to quantify the benefits and trade-offs of plant diversity to flower visitors can only be accomplished by considering the network of interactions that links wild plants, flower visitors and crop species as well as the potential for competition for soil resources.

Here we consider the advantages and disadvantages for conservation and agriculture of allowing ruderal plants to co-occur with a crop species. Our study crop was sunflower *Helianthus annuus* L., an economically important annual crop grown worldwide (FAO 2010),

widely planted in an area of north-east South Africa where only small patchy fragments of natural habitat remain. Our first objective was to characterize the composition and structure of plant-flower visitor food webs within sunflower plantations. Honeybees are the most abundant flower visitors to sunflowers worldwide (Nderitu *et al.* 2008), and flower visitors are known to be affected by distance to natural habitat and by floral diversity (Kohler *et al.* 2008; Ricketts *et al.* 2008); however, the positive effects of plant diversity are only likely to occur near high quality habitats (Kohler *et al.* 2008). Therefore, we expected that flower visitors will be negatively affected by distance to natural habitat and distance to managed honeybee colonies; and that benefits of floral diversity within farms will be only significant near natural habitat, the composition and structure of plant-flower visitor food webs changing with increasing isolation from natural habitat. The second objective was to understand if the presence of a diverse community of flower visitors affected the foraging behavior of honeybees (Weiss 1983). Previous work revealed that non-honeybee visitors made an important indirect contribution to sunflower pollination, by altering honeybee foraging patterns (Greenleaf & Kremen 2006). Therefore, we expected that interactions with different groups of flower visitors would enhance movement of honeybees among sunflower heads. The third objective was to understand how changes in plant-flower visitor communities affect sunflower production. The within-crop abundance of flower visitors is an important driver of the productivity of pollinator-dependent crops (Vazquez *et al.* 2005; Lonsdorf *et al.* 2009); moreover, although co-flowering plants can either compete for (Campbell & Matlon 1985) or facilitate pollination (Lopezaraiza-Mikel *et al.* 2007), ruderal plants are commonly seen as detrimental to crop productivity due to competition for soil resources (Weiss 1983, farmers' personal communication). Therefore, we expected that production would be lower in the absence of flower visitors; that sunflower visitor abundance

would be the most important driver of crop productivity; and that an increase in ruderal plant abundance would negatively affect crop productivity.

Our results show that although pollinators decline with distance to natural habitat, when ruderal plants are allowed to co-exist with pollinator-dependent crops, diverse flower visitors are able to persist in areas of cultivation fields isolated from natural vegetation, enhancing movement of honeybees among sunflowers and crop production.

Materials and Methods

This study was conducted in a commercial sunflower farming region located in Limpopo Province, South Africa (27° 57'S, 28° 32'E), during the 2009 sunflower flowering season (March - April). The study region (approx. 54000 ha) has been used for sunflower production for several decades, rotated annually with other annuals, such as maize (*Zea mays* L.) and sorghum (*Sorghum* sp.). Some farmers allow beekeepers to place managed honeybee colonies (average 27 colonies/site) near sunflower fields. Nine farming areas (c. 2km radius; hereafter farms) with similar soil characteristics, each with 2-4 sunflower fields (50-180 ha), and several small patches of natural habitat (semi-dry savanna, 8%-25% cover area), at least 2 km away from each other, were selected within the region. Two to seven plots (4x4 m, sunflower density of 10 plants/m²) were selected per farm to cover a range of distances from natural habitat and from managed honeybee colonies. Plots were at least 350 m away from the nearest neighboring plot and 600 m away from any water-body, leading to a total of 33 plots, which were planted with one of five hybrid sunflower cultivars widely used for oil production. All plots selected were subjected to

similar management practices (see plot details in Table S1 in Supporting Information), herbicides being applied annually before sowing. Insecticides are only applied in sunflower fields once every five years, but are used regularly when the fields are planted with sorghum or maize, the last insecticide application in our study plots being at least one year before data collection. In spite of herbicide application, patches of annual ruderal plants can be found within sunflower plantations. As our study plots selection maximized homogeneity of abiotic conditions (similar soil type and proximity to water-bodies) abiotic conditions are unlikely to vary much within farms. The location of ruderal plants is more likely related to occasional failures in herbicide application. Nevertheless, spatial autocorrelation of ruderal abundance and flower diversity was tested by comparing the fit of a null model with and without spatial autocorrelation structure (linear, gaussian, exponential and spherical variograms were considered). If residuals were significantly spatially autocorrelated, models were corrected accordingly (see Zuur *et al.* 2009). Spatial autocorrelation was equally considered in all statistical analyses described hereafter, and all analyses were performed using the software R (R Development Core Team 2010).

Objective 1 –To characterize plant-flower visitor communities within sunflower plantations

The sunflower peak flowering season (*i.e.* approx. 50% of florets of the majority of the sunflower heads are open) is short, with each plot being at the peak of flowering for a maximum of one week. Therefore, each plot was surveyed on two different days (once in the morning, 09h00-13h00, and once in the afternoon, 14h00-17h00) during the peak of flowering. To assess the abundance of ruderal plants, in each survey 16 quadrats (0.25 m²) were randomly placed

throughout each plot. All plant species were identified and their vegetation cover (%) and number of floral units were registered. For most species one floral unit corresponded to one flower, but for compound species (*e.g.* Asteraceae) one floral unit corresponds to 1 cm² of flowers, the minimum size needed to allow one medium-sized visitor to forage without preventing visitation in the adjacent floral unit. Sunflower flower abundance was constant throughout the plots (approx. 10 sunflower heads/m², with an average radius of 10 cm of flowering florets, leading to a total of 3142 floral units/m²).

In each survey, three locations (one for each of three observers) were randomly selected within the plot and all the sunflower heads at the peak of flowering that could be reached were observed for 4 minutes, during which all insects that touched the reproductive structures of those sunflowers were recorded. For each of the other flowering plant species present in the plot, observations (3 x 4 minutes) were also done, immediately after the sunflower observations. Total observation time per plant species was 24 minutes per plot. Each flower visitor specimen was counted once and collected for later identification when no potential visitors were nearby, to avoid disturbance. If the flower visitor escaped, usually it flew further than 3m, so we assumed it did not return to the plot within the 4 minute observation period. All Hymenoptera, Diptera and Coleoptera specimens were separated to species or morphospecies by professional taxonomists (see Acknowledgements). All other orders were sorted by the authors. To standardize visitor abundance data, the total number of specimens observed in the plot on a given plant species was divided by the number of floral units observed of that species and then multiplied by the total number of floral units in the plot. Any interaction detected outside of the observation periods was registered as a rare event (interaction frequency = 0.01). Data were used to construct plant-flower visitor food webs for each plot.

To characterize the visitation patterns within each plot, we calculated abundance and species richness of flower visitors, and network properties, such as generality (mean number of plant species per visitor), connectance (realized number of possible links between visitors and plants), linkage density (mean number of visitor specimens recorded per link), and interaction evenness (similarity of plant-visitor linkage density). Food web properties were calculated (package bipartite) using only the plots where more than one flowering ruderal species was present (26 plots). Changes in generality and connectance would indicate variation on the trophic diversity of visitors (*e.g.* replacement of more specialized by more generalized visitors); while changes in linkage density and interaction evenness would indicate that the different plant-insect interactions were unequally affected by the explanatory variables. To understand how these community properties change within sunflower plantations, generalized linear mixed model (GLMM, Gaussian error distribution) selection procedure was done where all combinations of explanatory variables (distance to natural habitat, natural habitat % cover, distance to hives, flower species richness and cultivar) and their interactions were considered (package nlme). As honeybees can have large foraging ranges (von Frisch 1967), farm was included as a random variable. The most parsimonious model was selected as that with the lowest Akaike information criterion with a second-order correction for small sample sizes, AICc (Burnham & Anderson 2002). If necessary, data were log transformed to standardize residuals. The distance from the center of each plot to the nearest patch of natural habitat and the cover (%) of natural habitat in each farm were measured using 2008 aerial photographs. Changes in landscape that occurred after the date of the photographs, but before the flower visitor surveys, were taken into account.

Objective 2- To understand how flower visitor diversity affects honeybee foraging behaviour

Honeybee behavior surveys were done immediately after the flower visitation surveys in all plots where visitors other than honeybees were common (26 plots). Following the methodology described in Greenleaf and Kremen (2006), honeybees foraging on sunflower were selected and followed until another visitor landed on the same sunflower head. The pair would then be observed for a maximum of 10 minutes and the behaviour of the focal honeybee (remained or flew to another sunflower head) was registered. If a third visitor landed in the sunflower head the observation was discarded. Visitors were divided in groups according to their taxonomic order, size (small [<0.5 x honeybee wingspan]; medium [$0.5 >> 2$ x honeybee] or large [>2 x honeybee]) and activity level (low vs. high). For 40 minutes, the maximum number of behavioral observations was done by three observers. Data of flower visitor groups for which we had at least 14 observations were analysed using GLMM with binomial error distribution, using type of interacting species as fixed factor and plot within farm as random variables. Models were corrected for spatial autocorrelation if necessary.

Objective 3- To understand how plant-flower visitor communities affect sunflower production

To identify the contribution of flower visitors to sunflower pollination, an exclusion experiment was set up by selecting 18 sunflower heads in each of 31 study plots; nine were left open and the remaining nine were isolated from any insect visitation by covering with a white nylon mesh bag (c. 1 mm mesh width) before any floret opened. Although bag characteristics minimize microclimate changes (Ball *et al.* 1992), to ensure standard seed development conditions, all bags were removed at the end of the flowering season. Sixty days later, when seeds had reached maturity, seed set was assessed. As sunflower are valued by farmers in terms of seed mass or oil

content (also proportional to seed mass), seed mass (*i.e.* weight) was used as a measure of productivity. To standardize among sunflower heads, all achenes were removed from the sunflower heads and 100 seeds were randomly selected from each and weighted. Productivity was compared using GLMM (Gaussian error distribution) with treatment (no visitors *vs.* all visitors) and cultivar as fixed variables and plot within farm as random variables. To evaluate if all cultivars were equally affected by the exclusion treatment, the interaction between treatment and cultivar was also included in the analysis.

To understand which characteristics of the flower visitor community and landscape most influence, hence better predict, sunflower production, variations in seed mass of sunflower heads exposed to visitors were analysed using a model selection procedure, whereby all combinations of variables potentially influencing production and their interactions were considered: distance to natural habitat, ruderal flower species richness and abundance (% cover), cultivar, flower visitor abundance and species richness. As only one of the plots sampled was from the cultivar Monsanto 6822, this cultivar was not included in the analysis. Moreover, as any negative effect on production via soil resource competition between the crop and ruderal plants could be buffered by a potential positive effect of flower diversity on pollinators, we also evaluated the contribution of ruderal plant abundance to the variance in seed set of sunflower heads that had been isolated from pollinators (bagged sunflowers), using GLMM with plot within farm as random variable.

Results

Objective 1 –To characterize plant-flower visitor communities within sunflower plantations

Forty-seven out of 69 flower visitor species present in sunflower plantations were foraging on sunflower heads, and were also feeding on another 21 flowering plant species found within the plots (see Table S2 and S3 for details). The most abundant visitors were honeybees, which were responsible for 84% of the visits to sunflowers.

Distance to natural habitat made a significant contribution to explaining the variance in flower visitor community models, the number of honeybees and other flower visitors visiting sunflowers dropping to 61% and 24% of their maximum at 1000 m, respectively, and species richness dropping to 57% (Fig. 1; see equations in Table 1). Although proximity to managed honeybee colonies slightly increased the number of honeybees (see Fig. S1), overall no significant influence of this variable on flower visitors was detected (Table 1).

Ruderal plant abundance was low throughout the plots (0.1-1% of plot floral abundance and 1-20% of cover) and neither ruderal abundance (cover %) nor flower diversity were significantly spatially auto-correlated (Contribution of best fitted variogram to the fit of the null model of abundance: L-ratio=0.01, $P>0.05$; diversity: L-ratio=0.22, $P>0.05$). While flowering ruderals did not significantly contribute to explaining the variance in sunflower visitor abundance, they did have a positive effect on the species richness of sunflower visitors, which was 100% higher in plots with high ruderal flower diversity (maximum number of flower species within plots was 10) than in plots with only sunflower (Table 1). The positive effect of flower diversity even ameliorated the negative effect of isolation from natural habitat: diversity of sunflower visitors in plots located at 1000 m from natural habitat but with 10 species of flowers

being on average 14% higher than diversity of plots located near natural habitat but with no wild flowers (5.7 species vs. 5.0 species visiting sunflower per plot, respectively, see equation in Table 1). However, the highest values of diversity occurred when both variables were optimized (10.0 species visiting sunflower in plots near natural habitat and with 10 species of flowers). Neither coverage of natural habitat within visitors foraging range nor cultivar significantly contributed to explain variance of flower visitor abundance or species richness. None of the network properties (connectance, generality, linkage density, interaction evenness) varied significantly with any of the explanatory variables considered in the analysis.

Objective 2- To understand how flower visitor diversity affects honeybee foraging behaviour

Six groups of visitors were commonly found foraging in the same sunflower heads with our focal honeybees: honeybees (139 observations); maize-beetles (medium size; low activity; 22 observations); flies (medium size; high activity; 14 observations); other bees and wasps (medium size; high activity; 22 observations); butterflies (large; high activity; 43 observations); moths (large; low activity; 30 observations). Maize-beetles (*Astylus atromaculatus* Blanchard), were the only medium-size Coleoptera for which we got interaction observation data. Interaction with other bee species, butterflies and moths significantly enhanced honeybee movement among sunflower heads (Table 2), with almost all (>90%) honeybees that interacted with other bee species or with butterflies and the majority (73%) that interacted with moths moving to another sunflower head. The majority of the honeybees that interacted with another honeybee or with maize-beetles remained foraging in the same sunflower head. Also when interacting with flies, the majority of honeybees (77%) moved, although this effect was non-significant.

Objective 3- To understand how plant-flower visitor communities affect sunflower production

As some control and experimental plants were found damaged, our final number of sunflower heads was 266 control and 260 experimental among all plots. The exclusion experiment revealed that sunflower visitors significantly contributed to pollination, with the seed mass of sunflower heads that had been isolated from flower visitors being significantly lower than of those heads exposed to normal insect activity (Likelihood ratio = 243.5, $P < 0.0001$). The increase in the average seed mass was consistent among all cultivars (Fig. 2), although cultivars Pannar 7533 and Monsanto DK4040 were significantly less affected than the remaining cultivars (Interaction Treatment-Cultivar: Likelihood ratio = 26.2, $P < 0.001$).

When analyzing variation in productivity throughout the farms, we found that seed mass declined significantly with distance to natural habitat (DN) and increased significantly with species richness of ruderal flowers (RFR) (see model 2 in Table 3). The positive effect of ruderal flower diversity was significant at any distance from natural habitat (Interaction DN*RFR: Likelihood ratio = 0.79, $P > 0.05$) and was independent of ruderal cover (Interaction RFR*Ruderal cover: Likelihood ratio = 0.14, $P > 0.05$). However, the variation in seed set was better explained by models based on flower visitor community characteristics (see model 1 vs. model 2 in Table 3). Visitor abundance and species richness are positively correlated ($\rho = 0.66$, $S = 2044.0$, $P < 0.001$), both having positive impacts on production when included in models separately (see models 1 and 6 in Table 3). However, production was better predicted by variation in species richness than by visitor abundance, increasing 47-74% from low (only honeybee) to high (14 species, the maximum number of species observed per plot) flower visitor diversity plots (Fig. S2, see equations in Table 3). Distance to managed honeybee colonies had no effect on sunflower production.

Analysis of variation of seed mass from sunflower heads that had been isolated from pollinators, and hence mostly influenced by abiotic conditions such as competition for soil resources (water and nutrients) with other plants, revealed that ruderal plant abundance (measured as the percentage of cover) did not significantly affect sunflower production (Likelihood ratio = 0.01, $n=260$, $P>0.05$).

Discussion

The balance between perceived costs and benefits of creating flower-rich patches within-crop fields to farmers of pollinator dependent crops is still unclear, such measures being rarely implemented in the absence of governmental subsidies (Ghazoul 2007). Our results show that if farmers allow ruderal plants to co-exist with pollinator-dependent crops, diverse flower visitors are able to persist in isolated areas of cultivation areas, benefiting production. Such benefits maximize the positive effects of the remaining patches of natural habitat. As ruderal plants in our study plots do not compete with sunflower for soil resources or reduce plantation area, this practice would bring no added costs to farmers, even reducing herbicide application costs. Therefore, if extensively applied this practice could benefit both biodiversity and agriculture. We consider the implications of these results for pollinator-dependent crop production and for conservation.

Objective 1 –To characterize plant-flower visitor communities within sunflower plantations

Consistent with previous studies (Nderitu *et al.* 2008; Greenleaf & Kremen 2006), the sunflower visitor community comprised a diverse number of species, but was dominated by honeybees. Honeybees (*Apis melliferae scutellata* Lepeletier) are native to the region and frequently nest in indigenous vegetation within the farm (Johannsmeier 2001). The lack of a negative effect of distance from colonies suggests that the use of managed honeybees does not compensate the loss of natural habitat. It is, however, possible that the introduction of honeybees would have a greater benefit in crop fields located in areas where natural habitat has been completely transformed.

As expected (Ricketts *et al.* 2008), distance to natural habitat had a negative effect on sunflower visitor abundance and species richness. However, contrary to our expectations, plant diversity had a positive effect both near and far from natural habitat, the diversity of flower visitors doubling from plots with only sunflower to plots with high flower diversity. As most flower visitors have limited foraging abilities, mostly foraging in a short radius around their nesting areas (Kohler *et al.* 2008), and since insecticides had not been applied in the study plots for at least one year (see methods), these results suggest that the presence of ruderal plants provided islands of resources, leading to the establishment of flower visitors in the middle of the agricultural landscape. In fact, although soil is plowed before plantation, active ground nests of wild bees were twice observed by us within sunflower plots that had high ruderal abundance, and Lepidoptera and Diptera species utilise diverse larval host plants (*e.g.* Smith 1976) potentially using the ruderal plants as a larval resource. A systematic survey of flower visitor nests/host plants would be necessary to fully understand the effect of ruderals on location of flower visitors' larvae. Moreover, in agreement with previous studies (Carvalho *et al.* 2010), cover of

natural habitat within the foraging range of flower visitors did not significantly affect sunflower visitation, suggesting that the presence of small fragments of natural habitat (minimum in our study was 8% cover within 2 km radius) were enough to sustain crop flower visitors.

The lack of variation of network descriptors suggests that ruderal plant diversity was sufficient to maintain the visitation patterns along a gradient of distance to natural habitat. These results agree with the hypothesis that weak interactions can confer stability on a community (Neutel *et al.* 2007; Banasek-Ritcher *et al.* 2009), dampening oscillations in structure and composition of the flower visitor community. Rare interactions may be crucial to compensate the low content in important nutrients that can result from a pure diet on an Asteraceae species (*e.g.* sunflower) (Muller & Kuhlmann 2008). Preserving flower visitor communities holistically and maintaining species involved in weak interactions may also ensure the ability to adapt to environmental changes (Lopezaraiza-Mikel *et al.* 2007), and therefore increase the resilience of pollination services. These findings highlight the importance of maintaining alternative plant species within crop fields. Nonetheless, abundance of visitors declined with distance to natural habitat, possibly because areas with permanent native vegetation ensure flower resources not only throughout the crop flowering season but throughout the year, also providing nesting sites (Tuell *et al.* 2008). Therefore, the benefits brought by the presence of wild plant species within crop fields will be maximized only if reservoirs of flower visitor diversity (*i.e.* natural habitat) are close by.

Objective 2- To understand how flower visitor diversity affects honeybee foraging behaviour

In agreement with Greenleaf and Kremen (2006), our results show that interactions with non-honeybee visitors enhanced honeybee movement among sunflower heads. The weaker effect of

the moths and maize-beetles could be related to the lower activity levels of these groups in comparison to bees, wasps and butterflies. The non-significant effect of flies is likely due to the low number of recorded interactions with this group. Although in our studied cultivars male and female flowers occur in the same sunflower head, they are located in different rings of the sunflower head and the majority of honeybees foraged in a localized region of the sunflower head (personal observation). Moreover, self-incompatibility mechanisms (Weiss 1983) limit the extent to which a given sunflower cultivar is able to self-pollinate. Therefore, it is likely that enhanced movement among sunflowers increases pollen flow, and hence pollination efficiency of honeybee individuals.

Objective 3- To understand how plant-flower visitor communities affect sunflower production

Sunflower cultivars are being continuously developed for greater self-pollination ability (Weiss 1983), which would imply a lesser role for insect pollinators. However, our exclusion experiment results are consistent with previous findings (Nderitu *et al.* 2008), by showing that maintaining an abundant and diverse community of flower visitors within farmland is essential to maximize the production of several commercially used sunflower cultivars.

Changes in sunflower productivity were better explained by changes in the species richness of the flower visitor community than by changes in visitor abundance. Previous studies on crop pollination show similar results (Klein *et al.* 2003; Hoehn *et al.* 2008). As visitor abundance and species richness were correlated, both being affected by distance from natural habitat, it is difficult to detect statistically a combined effect of both variables, this being the most likely scenario. Experiments involving the manipulation of diversity in the flower visitor community independently of its abundance would be necessary to clearly separate the roles of diversity and

abundance. Nevertheless, diversity of flower visitors can enhance pollination via several mechanisms (Klein *et al.* 2009). As non-honeybee visitors are a minority it is unlikely that the effect of diversity is due to the presence of more efficient pollinators (*e.g.* Changnon *et al.* 1993; Hoehn *et al.* 2008). The increase of honeybee movement between sunflower heads due to interactions with other flower visitor species is the likely cause for the positive effect of diversity on production. Pollen supplementation experiments would help clarify the importance of cross-pollination for the productivity of different sunflower cultivars, and surveys where both abundance and visitation rate are assessed would help clarify the indirect role of diversity on pollinator efficiency.

Concerning the potential trade-offs of maintaining wild plants within cropland, our results show that the presence of ruderal plants did not have a negative impact on sunflower production, but instead had an indirect positive effect via the effect on flower visitor diversity. Bagged sunflower may be less resource-limited than fully pollinated. However, analysis of productivity of open sunflower heads shows that the indirect positive effect of ruderal diversity was not buffered at high ruderal abundances. The lack of competition between ruderal plants and sunflower could be related to the characteristics of the sunflower tap-root system (Weiss 1983), which may enable them to access resource nutrients in deeper soil layers that are inaccessible to the ruderal plants (see Walter 1971). However, weeds may compete with sunflower sprouts if they exceed a certain abundance level. Further studies involving fields where no herbicides are used, would be necessary to clarify the extent of such positive effects. Nevertheless, our results concur with previous studies showing that weed density (Hawes *et al.* 2010) and deposition of heterospecific pollen (Morales & Traveset 2008) not always constrains crop productivity.

Implications for agriculture and conservation

The rising demand on food supply is driving an accelerated replacement of natural habitat by cropland, seriously compromising sustainable development. To minimize agricultural expansion, measures that maximize productivity in the existing farming areas need to be considered. The results of this study indicate that allowing the natural occurrence of wild plants within crop fields ensures that resources for flower visitors are restored to some extent, without the loss of arable land. Such practice not only helps sustain pollinator diversity, but also benefits production in sunflower crop areas which are isolated from natural habitat. Moreover, in our study approximately 50% of the wild flowers were native. Enhancing native flower diversity in relation to alien species could maximize the benefits to conservation (see Potts *et al.* 2010). Further studies are necessary to better understand the relationship between the composition of wild plant communities and the benefits to crop flower visitation. Such relationships are likely to vary across crop species and regions of the world (Kohler *et al.* 2007), depending on the nesting requirements and foraging ability of the resident flower visitors (Lonsdorf *et al.* 2009).

As proximity to natural habitat also benefits the drivers of productivity (flower visitors), the benefits of within-field plant diversity to overall production are likely to be maximized if combined with the restoration of natural patches within fields and if pesticide application is kept to a minimum. Such restoration areas will, however, compromise cultivation areas not only for sunflowers but also for other non-pollinator dependent annual crops that are rotated with sunflower. Nonetheless, it is possible that such crops also benefit from the presence of wild vegetation via other ecosystem services such as pest control (*e.g.* Isaacs *et al.* 2009). Studies that combine pollination with pest control surveys are needed to understand the cost-benefit relations of such restoration areas over several years.

Concluding remarks – By providing evidence of a crop yield improvement due to increased biodiversity (both insects and plants), this study contributes to the clarification of the value of biodiversity to crop production, providing an economic incentive for investment in pollinator-friendly farming practices. Even when abundance of an effective pollinator (honeybee) is maintained through the intense use of managed hives, in a region of the world where they are native and still unaffected by the major bee diseases/pests (Dietemann *et al.* 2009), pollinator diversity still makes an important contribution to crop pollination services. Such diversity can be enhanced by reducing herbicide application, allowing beneficial wild flowers to flourish throughout the crop fields. Ensuring the maintenance of diverse plant-pollinator communities within farmlands can help maximize land productivity, benefit nature conservation and increase the resilience of pollination services to future environmental perturbations.

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Table 1. Effect of landscape and management practices on sunflower visitors. The two most parsimonious models are listed according to AICc values and the equation of the best model (lowest AICc) is provided for each subset. Number of observations was 33 and groups of random variables were nine. *P*-values were obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. n.s., *P* > 0.05. Honeybee abundance and species richness models were corrected for spatial autocorrelation of residuals (exponential and spherical correlation structure, respectively). The residuals of all other models were not significantly spatially correlated. Distance values should be included in the model equation in meters. The symbol “-” represents a variable not included in the model. Interactions between explanatory variables did not contribute significantly to any of the models.

Response variable (Y)	DN <i>P</i> value	NC <i>P</i> value	DH <i>P</i> value	RFR <i>P</i> value	C <i>P</i> value	df	AICc	ΔAICc
<i>Honeybee abundance</i>								
Model 1 (best model)	<0.03	-	-	-	-	24	34.2	0.0
Model 2	<0.05	-	-	ns	-	23	36.8	2.6
Best model equation: $Y = e^{4.9916 - 0.0005 \times DN} - 1 \rightarrow$ 39% fewer honeybees at 1000 m								
<i>Other visitor abundance</i>								
Model 1 (best model)	<0.05	-	-	-	-	24	113.2	0.0
Model 2	<0.05	-	ns	-	-	23	115.6	2.4
Best model equation: $Y = e^{3.2726 - 0.0013 \times DN} - 1 \rightarrow$ 76% fewer visitors at 1000 m								
<i>Flower visitor species richness</i>								
Model 1 (best model)	<0.03	-	-	<	-	23	38.4	0.0
Model 2	<0.03	-	-	-	-	22	41.1	2.7
Best model equation: $Y = e^{1.7841 - 0.0005 \times DN + 0.0612 \times RFR} - 1 \rightarrow$ 43% fewer species from 0 to 1000 m 100% more species from single to high RFR (10 species)								

DN - distance to natural habitat, **NC** - natural habitat % cover within 2km radius, **DH** - distance to managed honeybee colonies, **RFR** - ruderal flower species richness, **C** - cultivar.

Table 2 – Effect of intra and interspecific interactions on honeybee (HB) foraging behaviour. ns – $P > 0.05$.

Interaction	HB movement to other sunflower head	Average foraging time before movement (sec)	Movement paired comparison with HB-HB interaction	
			z-test value	P-value
HB-HB	46%	101 ± 105	-	-
HB – maize-beetle	36%	145 ± 70	-1.37	ns
HB - fly	71%	86 ± 74	1.21	ns
HB - Other bee	91%	73 ± 43	2.43	<0.02
HB - Butterfly	93%	65 ± 69	4.47	<0.0001
HB - Moth	73%	101 ± 82	3.82	<0.0002

Table 3. Effect of distance to natural habitat (DN), ruderal flower species richness (RFR) and ruderal plant abundance (RA), sunflower flower visitor abundance (FVA) and species richness (FVR) and cultivar (C) on sunflower seed set. Number of observations was 259 and random variables (plot within farm) groups were 31. *P*-values were obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. n.s., *P* > 0.05. As FVA and FVR are driven by DN and RFR, to compare the contributions of the different sets of variables, the seven most parsimonious models are listed according to AICc values and the equation of the best model (lowest AICc) is provided for each cultivar. No significant spatial autocorrelation of residuals was detected in the models. The symbol “-” represents a variable not included in the model. Interactions between explanatory variables did not contribute significantly to any of the models.

Response variable (Y)	DN <i>P</i> value	RFR <i>P</i> value	RA <i>P</i> value	FVA <i>P</i> value	FVR <i>P</i> value	C <i>P</i> value	df	AICc	ΔAICc
<i>Seed set (weight)</i>									
Model 1 (best model)	-	-	-	-	<0.003	<0.02	25	808.3	0.0
Model 2	<0.03	<0.03	-	-	-	ns	24	810.5	2.2
Model 3	-	<0.004	-	-	-	-	28	812.7	4.4
Model 4	<0.005	-	-	-	-	ns	25	812.7	4.4
Model 5	-	-	-	-	<0.01	-	28	812.9	4.6
Model 6	-	-	-	<0.02	-	ns	25	813.1	4.8
Model 7	-	<0.02	-	-	-	ns	25	814.6	6.3
Best model:	Pannar 7033		Y = 4.4822+ 0.2311*FVR		62% increase from low (1 species) to high (14 species) FVR				
	Pannar 7355		Y = 3.7999+ 0.2311*FVR		74% increase from low (1 species) to high (14 species) FVR				
	Syngenta		Y = 5.0644+ 0.2311*FVR		55% increase from low (1 species) to high (14 species) FVR				
	Monsanto DK4040		Y = 6.0057+ 0.2311*FVR		47% increase from low (1 species) to high (14 species) FVR				

Figures

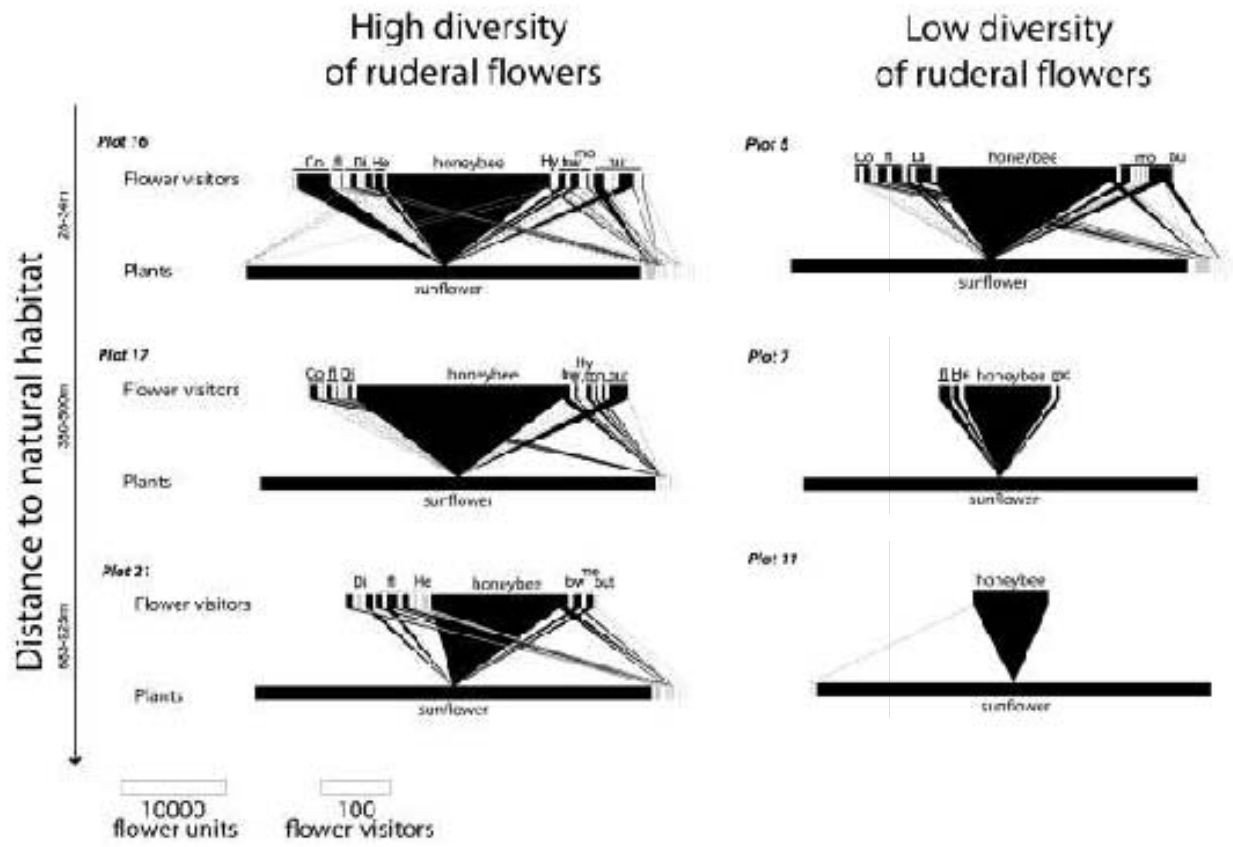


Figure 1

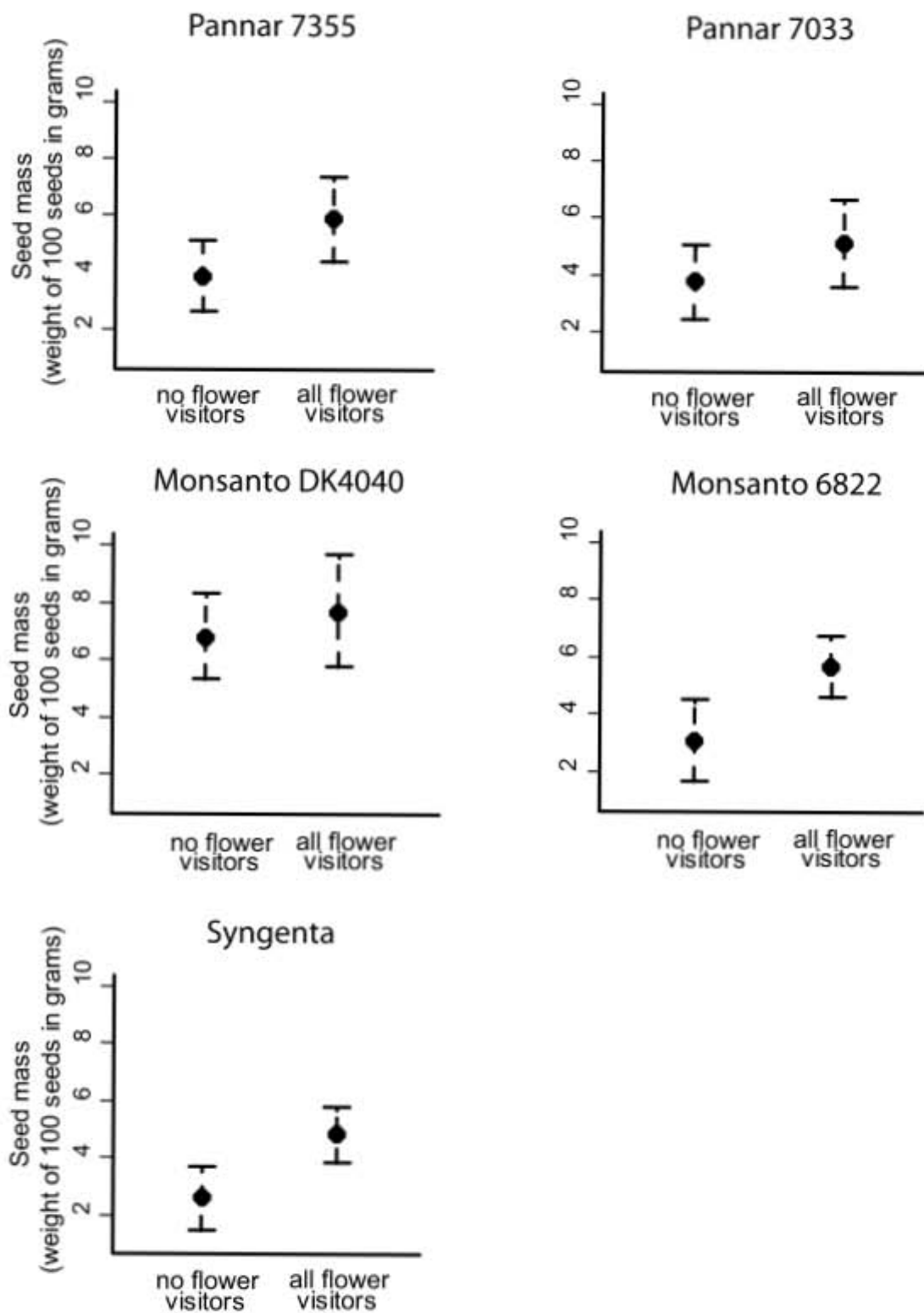


Figure 2

Figure legends

Figure 1. Effect of distance to natural habitat and of ruderal flowering plant diversity on sunflower flower visitation webs. The six plots here presented represent two sets of plots located within the same farm (5 and 3, respectively) and are located far (670-2000 m) from managed honeybee colonies and near (28-34m), at medium distance (380-500m) and far (879-925m) from natural habitat. Each species of plant and insect is represented by a rectangle. The overall list of species is provided in Tables S2 and S3. The widths of the rectangles represent overall species abundance per plot per survey and the size of the lines connecting them represents the number of insects visiting each plant species. Sunflower and its flower visitors are shown in black, while other species are presented in grey. Dashed lines represent rare interactions.

Figure 1 foot note: mb – maize-beetle (0.5-2 x honeybee wingspan; high activity); Co – other Coleoptera, fl – flies (0.5-2 x honeybee wingspan; high activity); Di – other Diptera; He – Heteroptera; bw – other bees and wasps (0.5-2 x honeybee wingspan; high activity); Hy – other Hymenoptera; mo - moths (> 2 x honeybee wingspan; low activity); but - butterflies (> 2 x honeybee wingspan; high activity).

Figure 2. Mean \pm standard deviation (whiskers) sunflower seed mass in different cultivars exposed to or isolated from flower visitors. Pannar 7355, n = 238; Pannar 7033, n = 188; Monsanto 6822, n = 14; Monsanto DK4040, n = 53; Syngenta, n = 33. Number of observations was 526 and random variable (plot within farm) groups were 31.

Supporting information

Title: Natural and within-farmland biodiversity enhances crop productivity

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Pirk, Christian W.W.; Donaldson, John S.; Nicolson, Sue W.

Table S1. Summary details of the sunflower plots used in this study.

Plot	Farm	Distance to natural habitat (m)	Distance to managed honeybees (m)	Ruderal plant abundance (% cover)	Cultivar	Seed set data available?
1	1	108	90	7	Pannar 7033	Yes
2	1	515	500	5	Pannar 7033	Yes
3	2	46	1350	6	Pannar 7033	Yes
4	2	487	1800	10	Pannar 7033	Yes
5	3	28	1300	10	Pannar 7355	Yes
6	3	30	85	12	Pannar 7355	yes
7	3	380	970	20	Pannar 7355	yes
8	3	404	560	5	Pannar 7355	yes
9	3	410	980	14	Pannar 7355	yes
10	3	601	1100	12	Pannar 7033	yes
11	3	683	670	5	Pannar 7355	yes
12	4	744	1900	4	Pannar 7355	yes
13	4	781	70	7	Syngenta	yes
14	4	1165	490	10	Syngenta	yes
15	4	1220	970	6	Syngenta	yes
16	5	34	2000	9	Pannar 7355	yes
17	5	500	1500	10	Pannar 7355	yes
18	5	540	1000	11	Pannar 7355	yes
19	5	765	1200	1	Pannar 7355	yes
20	5	780	540	12	Pannar 7355	yes
21	5	925	1050	6	Pannar 7355	yes
22	5	1000	100	6	Pannar 7355	yes
23	6	30	2300	14	Pannar 7033	yes
24	6	280	2200	20	Pannar 7033	yes
25	6	553	2100	12	Pannar 7033	yes
26	7	37	170	10	MonsantoDK4040	yes
27	7	461	550	12	MonsantoDK4040	yes
28	8	652	1070	14	Pannar 7033	yes
29	8	910	220	6	Pannar 7033	yes
30	8	923	1040	5	Pannar 7033	no

31	8	933	520	13	Pannar 7033	yes
32	9	45	340	10	Monsanto6822	no
33	9	184	539	18	Monsanto6822	yes

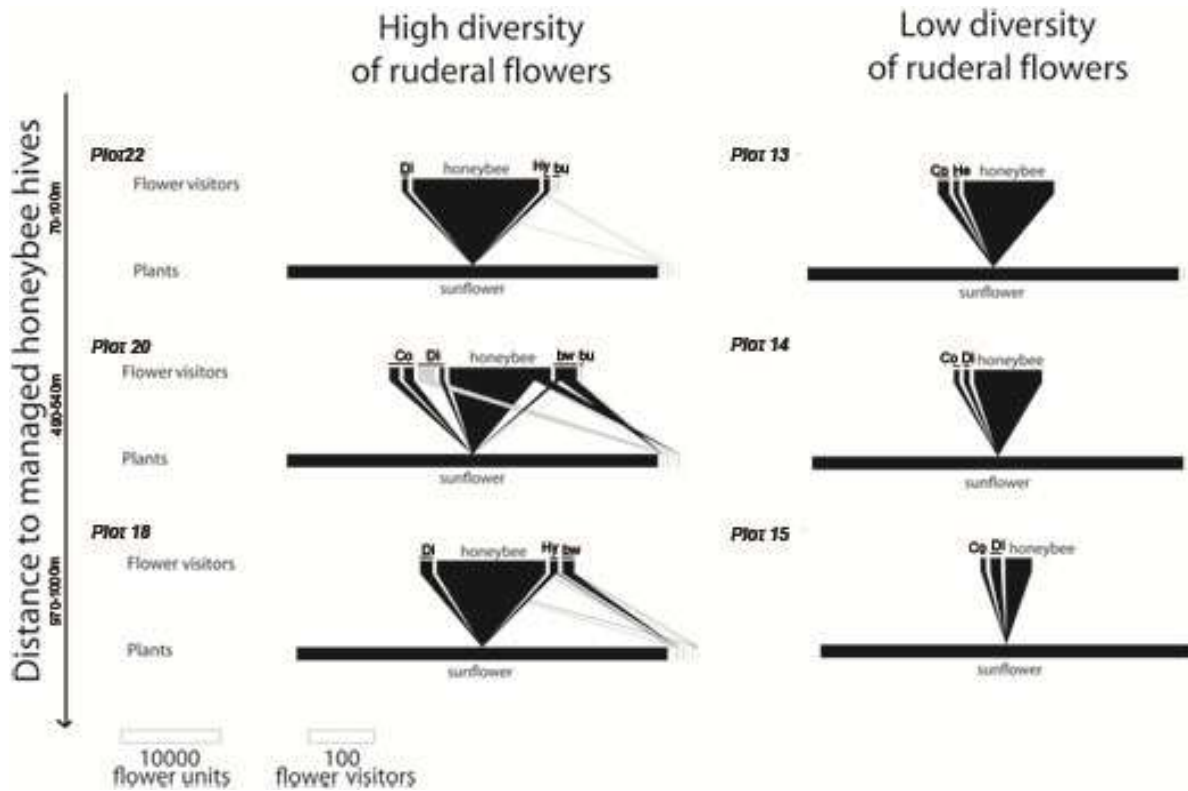
Table S2. List of flowering plants recorded during surveys in sunflower plots. * - alien plant

Code	Plant species	Plant family	Total number of visitors	Total number of floral units	Visitors per floral unit)
1	<i>Flaveria bidentis</i> (L.) Kuntze*	Asteraceae	82	230	0.36
2	<i>Helianthus annuus</i> L.*	Asteraceae	5115	969671	0.01
3	<i>Schkuhria pinnata</i> (Lam.) Kuntze ex Thell.*	Asteraceae	22	2066	0.01
4	<i>Senecio apiifolius</i> (DC.) Benth. & Hook.	Asteraceae	169	821	0.21
5	<i>Sonchus asper</i> (L.) Hill *	Asteraceae	0	2	0
6	<i>Tagetes minuta</i> L. *	Asteraceae	251	6853	0.04
7	<i>Bidens pilosa</i> L. *	Asteraceae	0	2	0
8	<i>Zinnia peruviana</i> (L.) L. *	Asteraceae	0	5	0
9	<i>Commelina erecta</i> L.	Commelinaceae	4	428	0.01
10	<i>Ipomoea coscinoperma</i> (Choisy) Hochst.	Convolvulaceae	8	133	0.06
11	Fabaceae sp.	Fabaceae	16	113	0.14
12	<i>Ocimum</i> sp. *	Lamiaceae	47	617	0.08
13	<i>Hibiscus trionum</i> L. *	Malvaceae	4	14	0.29
14	Euphorbiaceae sp.	Euphorbiaceae	38	23	1.65
15	<i>Cucumis anguria</i> L. var. <i>longaculeatus</i> J. H. Kirkbr.	Cucurbitaceae	2	9	0.22
16	<i>Sesamum triphyllum</i> (Asch.) Welw.	Pedaliaceae	5	32	0.16
17	<i>Kohautia cynanchica</i> DC	Rubiaceae	2	25	0.08
18	<i>Richardia brasiliensis</i> Gomes *	Rubiaceae	22	1035	0.02
19	<i>Cardiospermum grandiflorum</i> Sw.	Sapindaceae	0	5	0
20	<i>Datura ferox</i> L.	Solanaceae	0	9	0
21	<i>Solanum retroflexum</i> Dunal.*	Solanaceae	0	16	0
22	<i>Tribulus terrestris</i> L.	Zygophyllaceae	0	2	0

Table S3. List of flower visitors recorded during surveys in sunflower plots. “ni” – not identified. When it was not possible to separate specimens in morphospecies with accuracy (when specimens escaped or were damaged) specimens were grouped in morphospecies (Sarcophagidae sp., Calliophoridae sp., *Lasioglossum* sp. and Chalcidoidea sp.). Species that were considered for the honeybee behavioural observations are indicated in the ‘Order’ column: mb – maize-beetle (0.5-2 x honeybee wingspan; low activity); fl – flies (0.5-2 x honeybee wingspan; high activity); bw – other bees and wasps (0.5-2 x honeybee wingspan; high activity); mo - moths (> 2 x honeybee wingspan; low activity); but - butterflies (> 2 x honeybee wingspan; high activity). Reference specimens were kept in University of Pretoria or with the taxonomists.

Code	Insect	Family	Order	Relative abundance (%)	Importance to sunflower (% of visitors)
1	<i>Decaria</i> sp1	Chrysomelidae	Coleoptera	0.38	<0.01
2	<i>Monolepta citrinella</i> Jacoby	Chrysomelidae	Coleoptera	0.21	0.2
3	Coccinellidae sp1	Coccinellidae	Coleoptera	0.08	-
4	<i>Baris</i> cf. <i>atrocoerulea</i> (Boheman)	Curculionidae	Coleoptera	0.1	0.1
5	Lathrididae sp1	Lathrididae	Coleoptera	0.21	0.2
6	<i>Astylus atromaculatus</i> Blanchard	Melyridae	Coleoptera (mb)	5.23	5.8
7	Melyridae sp1	Melyridae	Coleoptera	0.17	0.2
8	<i>Carpophilus</i> sp1	Nitidulidae	Coleoptera	1.50	1.5
9	<i>Meligethes</i> sp1	Nitidulidae	Coleoptera	0.02	-
10	<i>Lagria</i> cf. <i>aeneipennis</i> Fåhraeus	Tenebrionidae	Coleoptera	0.56	0.5
11	Bombyliidae sp1	Bombyliidae	Diptera	0.03	-
12	Bombyliidae sp2	Bombyliidae	Diptera	0.01	-
13	Calliophoridae sp (<i>Chrysomya</i> sp. & others)	Calliophoridae	Diptera (fl)	0.47	0.2
14	<i>Rhyncomya</i> sp.	Calliophoridae	Diptera (fl)	0.01	<0.01
15	Conopidae sp1	Conopidae	Diptera	0.06	-
16	Empididae sp1	Empididae	Diptera	0.65	-
17	Empididae sp2	Empididae	Diptera	0.02	-
18	Sarcophagidae sp. (2 species at least)	Sarcophagidae	Diptera (fl)	0.77	0.4
19	<i>Betasyrphus adliagatus</i> Wiend.	Syrphidae	Diptera (fl)	0.68	0.2
20	<i>Eumerus obliquus</i> Fab.	Syrphidae	Diptera	0.48	0.1
21	<i>Senaspis haemorrhoea</i> Gerst.	Syrphidae	Diptera (fl)	0.16	0.2
22	<i>Betasyrphus</i> sp1	Syrphidae	Diptera (fl)	0.33	0.4
23	<i>Eristalinus taeniops</i> (Wied)	Syrphidae	Diptera (fl)	0.17	0.1
24	<i>Ischiodon aegyptius</i> (Wied)	Syrphidae	Diptera	0.13	-
25	<i>Eristalinus</i> cf. <i>plurivittatus</i> (Macq)	Syrphidae	Diptera	0.01	-
26	Syrphidae sp1	Syrphidae	Diptera	0.02	-
27	Tephritidae sp	Tephritidae	Diptera	1.37	0.5
28	Diptera sp1	Ni	Diptera	0.09	-
29	Diptera sp2	ni	Diptera	0.32	0.2
30	<i>Spilostethus pandurus</i> Scopoli	Lygaeidae	Heteroptera	0.08	<0.01

31	Lygaeidae sp1	Lygaeidae	Heteroptera	0.74	-
32	<i>Nezara viridula</i> L.	Pentatomidae	Heteroptera	0.96	0.6
33	Tingidae cf. sp1	Tingidae	Heteroptera	0.39	0.4
34	<i>Apis mellifera</i> L.	Apidae	Hymenoptera	77.12	83.8
35	<i>Tetraloniella apicalis</i> cf. (Friese)	Apidae	Hymenoptera (bw)	0.14	0.1
36	<i>Xylocopa inconstans</i> Smith cf.	Apidae	Hymenoptera (bw)	0.09	0.1
37	Braconidae sp1	Braconidae	Hymenoptera	0.01	-
38	Braconidae sp2	Braconidae	Hymenoptera	0.02	-
39	Chalcidoidea sp.	Chalcidoidea	Hymenoptera	0.21	-
40	Formicidae sp1	Formicidae	Hymenoptera	0.61	0.1
41	<i>Lasioglossum</i> sp.	Halictidae	Hymenoptera	1.86	0.9
42	<i>Lipotriches</i> sp. cf	Halictidae	Hymenoptera (bw)	<0.01	<0.01
43	<i>Systropha</i> sp1	Halictidae	Hymenoptera (bw)	0.01	<0.01
44	<i>Megachile frontalis</i> Fab. cf.	Megachilidae	Hymenoptera (bw)	0.14	0.1
45	<i>Campsomeris</i> sp1	Scoliidae	Hymenoptera (bw)	<0.01	<0.01
46	<i>Belanogaster</i> sp1	Vespidae	Hymenoptera	<0.01	-
47	Vespidae sp1	Vespidae	Hymenoptera (bw)	0.10	0.1
48	<i>Amata cerbera</i> L.	Arctiidae	Lepidoptera (mo)	0.11	0.1
49	<i>Utetheisa pulchella</i> L.	Arctiidae	Lepidoptera (mo)	0.50	0.5
50	<i>Eudalaca exul</i> Herrich-Schäffer cf.	Hepialidae	Lepidoptera (mo)	<0.01	<0.01
51	<i>Spialia</i> sp1	Hesperidae	Lepidoptera (but)	0.03	<0.01
52	Hesperidae sp1	Hesperidae	Lepidoptera (but)	0.17	<0.01
53	<i>Borbo</i> sp1	Hesperidae	Lepidoptera (but)	0.09	<0.01
55	<i>Spindasis victoriae</i> (Butler)	Lycaenidae	Lepidoptera	0.02	-
56	<i>Acraea horta</i> L.	Nymphalidae	Lepidoptera	0.02	-
57	<i>Cynthia cardui</i> L.	Nymphalidae	Lepidoptera (but)	<0.01	<0.01
58	<i>Hypolimnas misippus</i> L.	Nymphalidae	Lepidoptera (but)	1.12	1.2
59	<i>Junonia hierta</i> Fab.	Nymphalidae	Lepidoptera (but)	<0.01	<0.01
60	<i>Junonia oenone</i> L.	Nymphalidae	Lepidoptera (but)	<0.01	<0.01
61	<i>Papilio horta</i> L.	Nymphalidae	Lepidoptera	0.01	-
62	<i>Belenois thysa</i> Hopffer	Pieridae	Lepidoptera (but)	<0.01	<0.01
63	<i>Catopsilia florella</i> (Fab.)	Pieridae	Lepidoptera (but)	<0.01	<0.01
64	Pieridae sp1	Pieridae	Lepidoptera	0.11	-
65	<i>Macroglossum trochilus</i> (Hubner)	Sphingidae	Lepidoptera	0.42	0.3
66	Heterocera sp1	ni	Lepidoptera	0.39	-
67	Heterocera sp2	ni	Lepidoptera	0.01	-
68	Heterocera sp3	ni	Lepidoptera (mo)	0.03	<0.01
69	Heterocera sp4	ni	Lepidoptera (mo)	0.23	0.3



mb – maize-beetle (0.5-2 x honeybee wingspan; high activity); Co – other Coleoptera, fl – flies (0.5-2 x honeybee wingspan; high activity); Di – other Diptera; He – Heteroptera; bw – other bees and wasps (0.5-2 x honeybee wingspan; high activity); Hy – other Hymenoptera; mo - moths (> 2 x honeybee wingspan; low activity); but - butterflies (> 2 x honeybee wingspan; high activity).

Figure S1. Effect of distance to managed honeybee colonies and of ruderal plant flowering diversity on sunflower flower visitation webs. The six plots here presented represent two sets of plots located within the same farm and are located far (540-1220m) from natural habitat and near (70-100m), medium distance (490-549m) and far (970-1000m) from introduced honeybee colonies (see plot details in Table S1). Each species of plant and insect is represented by a rectangle. Each species of plant and insect is represented by a rectangle. The list of species is provided in Tables S2 and S3. The widths of the rectangles represent overall species abundance per plot per survey and the size of the lines connecting them represents the number of insects visiting each plant species. Sunflower and its flower visitors are shown in black, while other species are presented in grey. Dashed lines represent rare interactions.

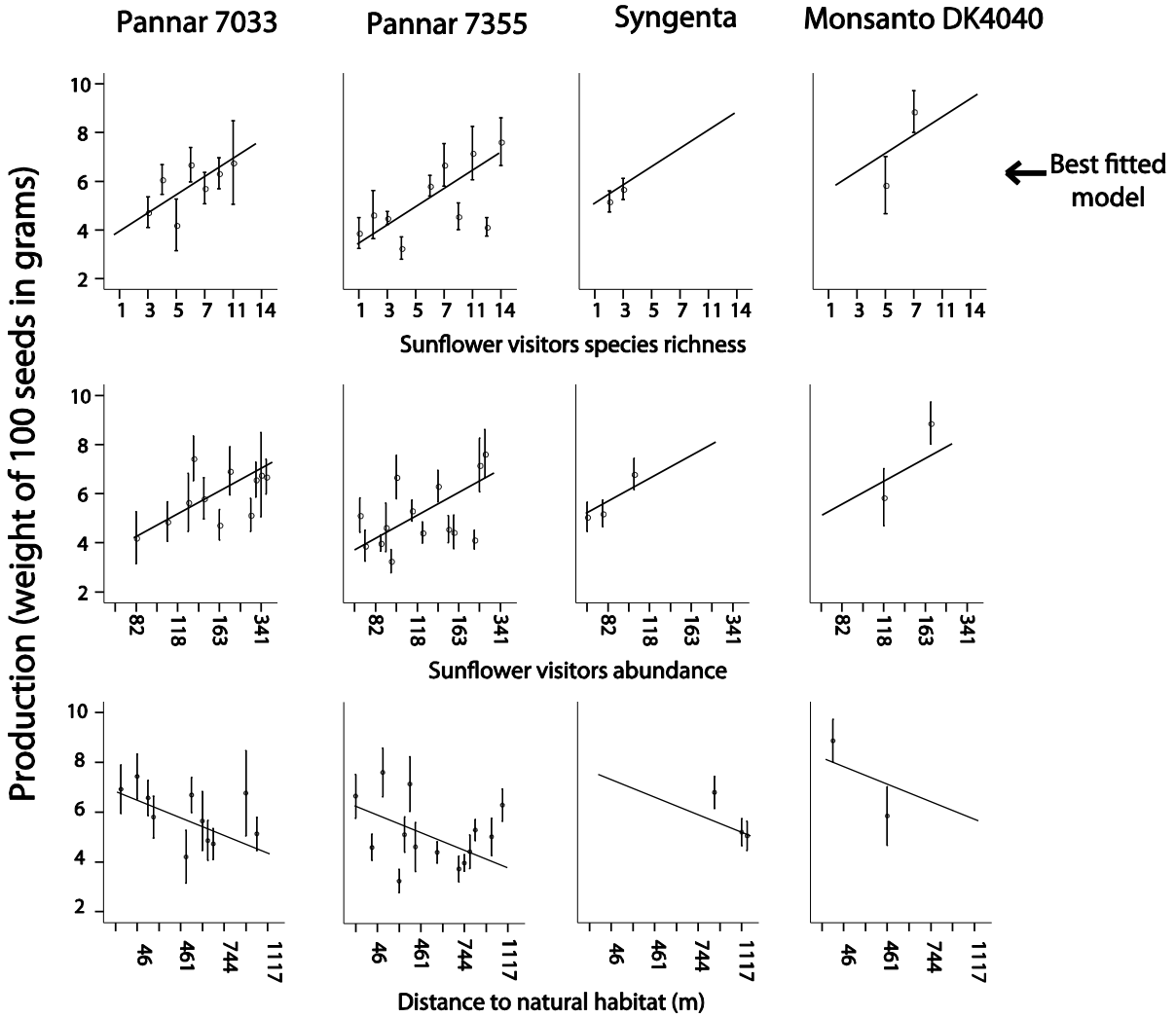


Figure S2. Variation of average sunflower production (whiskers: standard error of production within each plot) with distance to natural habitat, sunflower visitor abundance and species richness for the four main sunflower cultivars used in the study region. Model details are provided in Table 2. Total number of observations: Pannar 7033 – 94; Pannar 7533 – 122; Syngenta – 27; Monsanto DK4040 – 15.