

## LETTER

# Insect pollination is at least as important for marketable crop yield as plant quality in a seed crop

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### Abstract

The sustainability of agriculture can be improved by integrating management of ecosystem services, such as insect pollination, into farming practices. However, large-scale adoption of ecosystem services-based practices in agriculture is lacking, possibly because growers undervalue the benefits of ecosystem services compared to those of conventional management practices. Here we show that, under representative real-world conditions, pollination and plant quality made similar contributions to marketable seed yield of hybrid leek (*Allium porrum*). Relative to the median, a 25% improvement of plant quality and pollination increased crop value by an estimated \$18 007 and \$17 174 ha<sup>-1</sup> respectively. Across five crop lines, bumblebees delivered most pollination services, while other wild pollinator groups made less frequent but nevertheless substantial contributions. Honeybees actively managed for pollination services did not make significant contributions. Our results show that wild pollinators are an undervalued agricultural input and managing for enhancing pollinators makes sense economically in high-revenue insect-pollinated cropping systems.

### Keywords

Agricultural management, agro-ecology, crop pollination, crop yield, functional groups, species richness, structural equation modelling, visitation rate.

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## INTRODUCTION

Agriculture depends critically on ecosystem services such as nutrient cycling, pest regulation and animal pollination. Paradoxically, these ecosystem services are increasingly being degraded by agricultural practices that aim to increase crop production (Tilman *et al.* 2011; Deguines *et al.* 2014; Wagge *et al.* 2014). For example, 70% of the world's crops benefit from animal pollination (Klein *et al.* 2007), but at the same time agricultural intensification is one of the key drivers of the decline of wild pollinators in many parts of the world (Allen-Wardell *et al.* 1998; Kremen *et al.* 2002; Potts *et al.* 2010). Sustainable production of food, feed and fuel therefore requires solutions that integrate the management of ecosystem service-providing species into day-to-day agronomic management. This so-called ecological intensification of agriculture has been embraced by the scientific community and policy makers, in part because it potentially unifies crop production with biodiversity conservation in agricultural landscapes (Bommarco *et al.* 2013). However, the approach has seen little uptake among the main target group that should be implementing the practices, the agricultural sector (IPBES 2016). One of the reasons may be that they are unaware of the contribution of wild pollinators or underestimate its importance compared to conventional agricultural inputs (Munyuli 2011; Hanes *et al.* 2015). While the evidence base for the contribution of wild pollinators to crop production is substantial

(Garibaldi *et al.* 2013, 2016; Kleijn *et al.* 2015), little is known about how important that contribution is relative to that of typical agricultural management such as irrigation, or application of fertilizers and pesticides.

Recently, studies have started examining whether the contribution of insect pollination is influenced by agricultural management (van Gils *et al.* 2016; Tamburini *et al.* 2016; Garibaldi *et al.* 2018). However, it is difficult to infer real-world comparative effect sizes of pollinators and agricultural inputs from these studies because they used artificial settings (e.g. potted plants) or unrealistically large treatment contrasts (e.g. with and without pollinators; Garibaldi *et al.* (2018)). Whether managing for enhanced pollination makes sense agronomically and economically, depends essentially on whether a realistic increase can be obtained compared to the actual 'business as usual' situation, rather than a situation without pollination. This can only be determined in farming systems along realistic gradients in insect pollination and agricultural management (Garibaldi *et al.* 2016). Furthermore, the relative contributions of wild pollinators and input-based management should be robust across crop varieties that are available to farmers. Crop varieties not only differ markedly in their response to traditional agricultural inputs such as fertilizers (Guarda *et al.* 2004) but also with respect to dependence on insect pollination (Klatt *et al.* 2014). An assessment of the agronomic potential of using pollination as an agricultural input should therefore ideally take into account the variation in responses of different varieties.

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The contribution of pollination to agricultural production is at least partly determined by the composition of the pollinator community that is visiting the crop flowers. A higher species richness of crop visiting pollinators is often related to higher crop yields (Klein *et al.* 2003; Frund *et al.* 2013; Blitzer *et al.* 2016; Garibaldi *et al.* 2016), for example, through functional complementarity (Hoehn *et al.* 2008), or larger spatial (Winfree *et al.* 2018) and temporal (Garibaldi *et al.* 2011a) stability of yield. Other studies suggest that crop pollination mainly depends on the services provided by just a handful of the most abundant species (Kleijn *et al.* 2015; Winfree *et al.* 2015). Furthermore, different insect pollinators may be more or less effective for particular crops (Rader *et al.* 2013, 2016). For example, long-tongued bumblebees (*Bombus* sp.) are the most important pollinators for field bean pollination (Garratt *et al.* 2014), and red mason bees (*Osmia rufa*) are more efficient pollinators than hoverflies in oilseed rape (Jauker *et al.* 2012). The diversity or visitation rate of specific pollinator groups may therefore be more strongly linked to crop yield than that of all pollinators combined.

To test if it is more productive for a farmer to manage for better plants or to manage for more pollinators and how this varies between crop varieties, we used five female genetic lines in each of 36 commercial hybrid leek (*Allium porrum*) seed production fields in France and Italy. The fields were located in representative agricultural landscapes to obtain a realistic level of variation in abundance and species richness of crop visiting insect pollinators. We used plant quality, measured as basal circumference, as a proxy for agricultural management since the crop plant integrates all interacting effects of management and environmental conditions and is therefore arguably the best indicator of successful management by farmers. We formed an *a priori* conceptual framework which we used in Structural Equation Modeling (SEM). To establish which functional group contributed most to pollination and how this compared to the relative contribution of plant quality to marketable seed yield, we ran multiple SEMs for each female line with visitation rate and species richness of different functional groups. The average effect sizes of variables across the best SEMs of the five lines then indicates the relative contribution of plant quality and pollination for yield of hybrid leek seed production in general, while a comparison of the best SEM per line shows how the relative contribution of plant quality and pollination, and which functional groups are contributing most to yield varies between crop lines.

## MATERIALS AND METHODS

### Study system

We used commercial leek (*Allium porrum*) seed production fields as our study system. High-yielding leek varieties are produced in hybrid seed production systems (Wright 1980) that cross inbred, fully fertile (male; produces pollen) lines with inbred, male sterile (female; no pollen) lines. Each inbred line is commercially selected for specific characteristics of the variety that results from the cross between the two inbred lines. Fields contain a single male and a single female line and pollen is predominantly transferred by insects, making insect

pollinators essential for seed production (Brewster 2008). In our study regions, seeds are produced in southern Italy on small (0.5–2 ha) open fields, and in the Loire region in western France in semi-open tunnels (*c.* 0.1 ha). Honeybee colonies are placed in leek seed production fields in Italy, but not in France. In four French sites, bumblebee colonies (*Bombus terrestris*) were placed in the semi-open tunnels. Prior to each growing season, the seed company provides each grower with the same planting and cultivation protocol, but nevertheless considerable differences in management practices exist between fields due to, for example, differences in planting time or soil type.

### Experimental setup

In autumn 2015, we selected 18 fields in Italy (study area  $\pm 615 \text{ km}^2$ ) and 18 fields in France (study area  $\pm 1800 \text{ km}^2$ ) in landscapes located along a gradient of cover of potentially suitable pollinator habitat to obtain a representative level of variation in species richness and abundance. Pollinator habitat cover (mainly semi-natural grasslands, scrublands and woodlands; mean cover  $22\% \pm 19.2 \text{ SD}$ ) was estimated using satellite images. Except for one pair of fields that was separated by *c.* 850 m, all fields were located at least one kilometre from other selected fields, which is beyond the foraging range of most bees (Greenleaf *et al.* 2007). In each of the 36 fields, we planted five plants of five female production lines each in random order in a row or bed of the commercially grown female plants (*i.e.* 25 plants per field; female-lines coded B-F for this project). The plants were cultivated in the same way as the commercial plants.

### Pollinator observations

We used plant observations to estimate pollinator visitation rate as a proxy for pollination (Fijen & Kleijn 2017; Garibaldi *et al.* 2018). We selected two representative plants per line in each field, which we observed throughout the flowering period of *c.* 3 weeks in June–July 2016. We observed the primary flower head (umbel) of each plant for 20 min and recorded each pollinator that landed (bees and hoverflies; identified to the lowest taxonomic level possible). We repeated these observations at least three times (range: 3–5 times, mean: 3.3 times) throughout the flowering period with a minimum of four days between observations. Observations were carried out in dry circumstances, temperatures above 20 °C and wind speeds below five Beaufort (< 8 m/s). To estimate pollinator species richness, we performed transect counts at the field level, since plant observations underestimate species richness (Westphal *et al.* 2008; Fijen & Kleijn 2017). On each plant observation day, counts were done in a single fixed transect per field totaling 150 m<sup>2</sup>, divided into three continuous sub-transects of 50 m<sup>2</sup> (50 × 1 m). In each sub-transect, we counted all pollinators (bees and hoverflies; identified to the lowest taxonomic level possible) on female plants in 5-min net observation time, excluding catching and handling time (*i.e.* 15 min per transect). Pollinators that could be identified on the wing were counted in the field. All other pollinators were caught and stored for later identification. We considered *Bombus terrestris*

and *B. lucorum* as a single taxon c.f. Williams *et al.* (2012). Furthermore, we assumed that all individuals of *B. terrestris* came from the wild as the number of managed *B. terrestris* individuals was small compared with the average total number of individuals per field (up to 60 workers vs. 1267 individuals).

### Plant quality

Agricultural management consists of all measures taken and inputs used by growers to optimise plant size and vigour under the specific growing conditions of their farm (Sørensen *et al.* 1995). Plant size and vigour, in turn, are generally strongly related to seed production (Major 1980). We therefore measured several characteristics describing plant size and/or vigour: circumference of the pseudo stem at the base (basal circumference, rounded off to the nearest 5 mm), number of green leaves, height of the plant from the ground to the base of the umbel (height, to the nearest 1 cm), diameter of the flower stem 5 mm below the base of the umbel (flower stem diameter, to the nearest 0.01 mm) and the diameter of the umbel (umbel diameter, to the nearest 0.1 mm). Diameter was measured with a digital calliper. Height and circumference were measured with a tape measure. We measured each observed experimental plant and averaged measurements of each line in each field.

### Marketable seed yield

The individually marked plants were harvested just before seed shedding. For each line in each field, we pooled the two umbels and, after drying, threshed and cleaned by hand. All seeds were then counted with a seed counter (Contador, Pfeuffer GmbH). In one field, only one umbel of line F could be harvested and we doubled the seed count of that umbel for comparison. For unknown reasons, three plant pairs (two line B, one line C; all different fields) produced < 1% of the average marketable seeds and these were excluded from the analysis. Seed quality was determined with a vigour test for each line in each field. In this test, three sets of 100 randomly selected seeds were sown in suboptimal circumstances and after 18 days, the vigour of the seedlings was assessed by experts in a NAL-authorized test (Naktuinbouw Authorized Laboratory). Vigour was categorised as (A) optimal, (B) sub-optimal, (C) poor or (D) did not emerge. The average vigour scores (%) were calculated over the three sets. Usually, only seeds with vigour A or B are commercially sold. In practice, however, a too high proportion of vigour B plants is undesirable, depending on the quality standards of the company. For our study, we assumed that all vigour A or B plants will be sold. Marketable seed yield was therefore calculated as the total number of seeds per line per field multiplied by the percentage seeds that were scored as vigour A or B.

### Analysis – Structural equation modeling

Plant variables were generally correlated with one another. We therefore chose to include only basal circumference as a proxy for plant quality in subsequent analyses because this

variable was most strongly correlated with the other measured variables (Table S3), and because it can more easily be used by the agricultural sector than the other variables, as other variables only become apparent relatively late in the growing season. Pollinator visitation rate was calculated as the average of all observations per female line per field. In addition to calculating visitation rates for all visitors combined, we also calculated separate visitation rates for honeybees (*Apis mellifera*) and the functional groups of bumblebees (*Bombus* sp.), solitary bees (mostly Halictidae and Andrenidae) and hoverflies (Syrphidae), resulting in five different visitation rates per line per field. For a measure of species richness effects, we first corrected for the difference in effort of finding new pollinator species between fields using the Chao1 estimator for calculating estimated species richness per field (Chao *et al.* 2009). We calculated estimated species richness of all pollinators, as well as for each of the functional groups separately (except for honeybees as they only comprise one species). In total, we estimated species richness for four groups (all species and three functional groups) per field, and five different visitation rates (all species, three functional groups and honeybees) resulting in 20 combinations of visitation rate and estimated species richness per female line. Preliminary analyses showed that the ranges of all measured variables largely overlapped between the two countries and the results were qualitatively similar when countries were analysed separately. We therefore pooled the data for the final analysis. We standardised all variables before analysis to enable the comparison of the relative contribution of plant quality, pollinator visitation rate and pollinator richness on marketable seed yield.

We used Structural Equation Modeling (SEM; R-package ‘lavaan’ (Rosseel 2011; R Core Team 2018)) to estimate the relative importance of (different groups of) pollinators and plant quality. We first established a conceptual model of interactions with *a priori* hypotheses. We expected that three general factors were of importance in determining seed yield: plant quality, visitation rate of (different groups of) pollinators and species richness of (different groups of) pollinators. For each of the 20 candidate models per line, we included direct effects of plant quality, visitation rate of a single group of pollinators, and estimated species richness of a single group of pollinators on marketable seed yield in our SEMs. We also included indirect effects of high quality plants attracting more individuals of pollinators. Furthermore, visitation rate and species richness are usually correlated, so we also tested this correlation in our model.

For all models, we computed bootstrapped standard errors and test statistics. We used the chi-square, and the root mean square error of approximation (RMSEA) fit statistics to evaluate the model fit and discarded models that did not show an acceptable fit (Schermelleh-Engel *et al.* 2003). Because we were interested in which model explains the marketable seed yield best, we selected the best model based on the highest  $R^2$  (Grace 2006; Weston & Gore 2006). We calculated the standardised effect sizes using the path coefficients for each factor (Grace 2006). To establish the relative importance of plant quality, visitation rate and species richness across lines, we averaged the standardised effect sizes of the best model per female line.

### Analysis – economic contribution

Standardised effect sizes poorly demonstrate the practical implications of scientific results. To illustrate the real-world impact of our findings, we therefore estimated the economic contribution of changes in plant quality, pollinator visitation rate and pollinator richness. For this we required the unstandardised values of the factors to calculate the increase in marketable seed yield for each unit increase of the factor (e.g. one species extra increases marketable seed yield by  $n$ -seeds). We used the specific functional groups selected in the best model per line (Fig. 2 & Table 1) and used the parameter estimates of a SEM based on the unstandardised values. We calculated the contribution to the value of the marketable seed yield for the whole range of the observed factors of the best models per line (Table S1 & S2). Leek seed prices from our collaborator or competitors are undisclosed information, and commercial seed prices were only available for the 28 worldwide leading crops and not for leek (Kynetec 2017). We therefore assumed leek seed prices were similar to those of related onion (*Allium cepa*) seeds. For our calculations, we used the average seed price (\$0.00144 seed<sup>-1</sup>) of hybrid onion seed in 24 European countries from 2016 (Kynetec 2017). Leek seed production fields have on average a plant density of 110,000 plants per hectare, of which two-third are hybrid seed-producing female plants (average density 7.3 female plants/m<sup>2</sup>; c.f. Brewster (2008)). Using these values, we calculated the economic contribution of each factor per hectare ( $E$ , \$ ha<sup>-1</sup>) for each line as:

$$E = \frac{p * i * v * d}{2}$$

where  $p$  is the unstandardised parameter estimate (the slope predicting the number of seeds),  $i$  the increase in units from the low range to the high range (in cm, pollinators minute<sup>-1</sup>, or species),  $v$  the market value (\$ seed<sup>-1</sup>) and  $d$  the number of female plants per hectare (plants ha<sup>-1</sup>). As we used two plants per line per field in our experiment, we divided the equation by two.

To estimate the effects of a management improvement that can be realistically achieved by growers, we calculated for each factor what the increase in marketable seed yield would be if this factor would change from the median to the 75th percentile of the observed range. This resulted in an economic contribution for each line, and we averaged these contributions to draw general conclusions on the value of plant quality, pollinator visitation rate and pollinator richness on marketable seed yield, based on achievable within-range improvements.

## RESULTS

### Between field variation in crop pollinators and plant quality in a real-world farming system

In 394 h of observing the umbels of our experimental plants, we counted a total of 1 471 flower visiting pollinators. Even though the five female lines were planted within one metre of one another, the observed average visitation rate differed

substantially between functional groups and lines, and ranged from 0.00 to 0.63 pollinators per minute (Table S1). The most frequent visitors were pollinator species that can be commonly found on crops throughout Europe (Kleijn *et al.* 2015): *Bombus terrestris* (25.4%), *Apis mellifera* (13.9%), *Andrena flavipes* (12.1%), *Lasioglossum malachurum* (7.0%) and *Bombus lapidarius* (6.9%). The field-level transect surveys confirmed the presence of considerable differences in the pollinator communities between the examined leek fields. Estimated species richness of all pollinators combined was high compared with other studies (Garibaldi *et al.* 2016) with 27.9 (SE: 1.3 SE) species per field but showed a wide range between fields from a minimum of only seven to a maximum of 113 species per field. Not all functional groups contributed equally to the species richness of the pollinator communities. The most species-rich group were the solitary bees, accounting for approximately half of the species (Table S2). Bumblebees made up 55% of the individuals at field level but were present with a mere 2.6 (SE: 0.2 SE) observed species per field. This functional group was dominated by the buff-tailed bumblebee *Bombus terrestris* and to a lesser extent the red-tailed bumblebee *B. lapidarius*. Together, these two species comprised 99% of all observed bumblebees in both the transects and the plant observations.

We used basal circumference as our proxy of plant quality as it was most strongly correlated with the other measured plant variables (see also Methods; Table S3). Plant quality varied considerably between fields and increased at least two-fold from lowest to highest quality plants in all lines (Table S1), showing that important differences in plant growth conditions existed although all farmers received the same growing protocol.

### The relative importance of pollination and plant quality on marketable seed yield

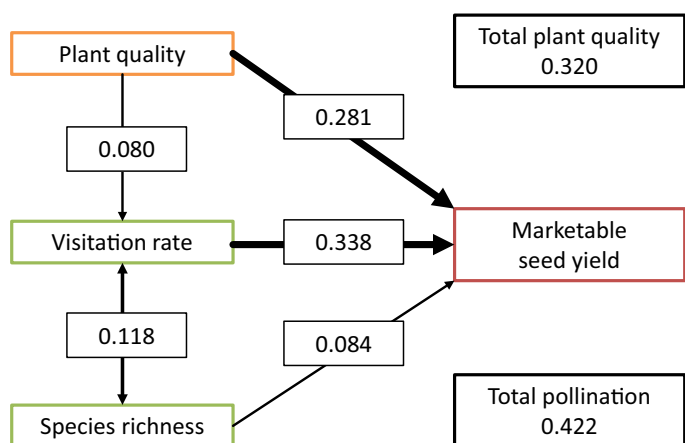
Across all five lines, marketable seed yield increased at least as strongly with pollination as with plant quality (Fig. 1). Effects of pollination and plant quality were mostly direct, with only one line showing a strong indirect effect of better quality plants attracting more pollinators, which in turn increased seed yield (line B; Fig. 2). The most consistent contributors to marketable seed yield were plant quality and bumblebee visitation rate with important contributions in four out of five lines (Fig. 2). Bumblebee visitation rate was included in more than half of the top five models that explained most of the variation in seed yield in the five lines (Table 1). In the fifth line, visitation rate of solitary bees explained yield variation best (Line E; Fig. 2). Visitation rate of all pollinators combined rarely featured in the models best explaining variation in marketable yield (Table 1). Similarly, visitation rates of honeybees *Apis mellifera* hardly contributed to crop yield as indicated by their inclusion in only two of the top models explaining variation in marketable seed yield (Table 1).

Species richness of hoverflies made an important contribution to marketable seed yield in two lines and species richness of all pollinators combined was important for seed yield of another line (Fig. 2). Species richness of hoverflies featured in

**Table 1** The top five SEM models for each combination of pollinator group visitation rate and species richness per crop line

Line	Rank	Visitation rate	Species richness	R <sup>2</sup>	Plant quality >	Plant quality >	Total effect plant quality	Visitation rate >	Species richness >	Visitation rate <>	Species richness <>
					Marketable seed yield	Visitation rate	quality	Marketable seed yield	Marketable seed yield	Species richness	Species richness
<b>B</b>	<b>1</b>	<b>Bumblebees</b>	<b>Hoverflies</b>	<b>0.320</b>	<b>0.090 (-0.263-0.442)</b>	<b>0.426 (0.188-0.665)</b>	<b>0.306 (-0.062-0.673)</b>	<b>0.507 (0.206-0.808)</b>	<b>-0.201 (-0.537-0.135)</b>	<b>0.132 (-0.177-0.382)</b>	
	2	Bumblebees	Solitary bees	0.305	0.146 (-0.180-0.471)	0.422 (0.205-0.639)	0.347 (0.021-0.674)	0.477 (0.148-0.806)	-0.038 (-0.355-0.279)	0.127 (-0.161-0.414)	
	3	Bumblebees	All pollinators	0.303	0.150 (-0.208-0.507)	0.410 (0.173-0.646)	0.344 (-0.005-0.692)	0.474 (0.141-0.807)	-0.041 (-0.517-0.435)	0.103 (-0.168-0.374)	
	4	Hoverflies	Solitary bees	0.220	0.378 (0.052-0.703)	0.097 (-0.296-0.490)	0.347 (-0.003-0.698)	-0.316 (-0.689-0.057)	0.017 (-0.266-0.300)	0.002 (-0.150-0.154)	
	5	Hoverflies	All pollinators	0.218	0.379 (0.053-0.704)	0.109 (-0.315-0.533)	0.344 (-0.015-0.703)	-0.319 (-0.675-0.037)	0.028 (-0.356-0.413)	0.078 (-0.053-0.210)	
<b>C</b>	<b>1</b>	<b>Bumblebees</b>	<b>Hoverflies</b>	<b>0.223</b>	<b>0.233 (-0.156-0.621)</b>	<b>-0.131 (-0.510-0.248)</b>	<b>0.175 (-0.244-0.593)</b>	<b>0.441 (0.116-0.765)</b>	<b>0.048 (-0.232-0.328)</b>	<b>-0.024 (-0.237-0.188)</b>	
	2	Bumblebees	Bumblebees	0.222	0.229 (-0.149-0.606)	-0.125 (-0.453-0.203)	0.176 (-0.230-0.581)	0.424 (0.084-0.764)	0.037 (-0.355-0.430)	0.404 (0.148-0.660)	
	3	Bumblebees	All pollinators	0.221	0.230 (-0.145-0.605)	-0.130 (-0.477-0.218)	0.173 (-0.220-0.567)	0.439 (0.147-0.732)	-0.023 (-0.566-0.520)	-0.006 (-0.160-0.147)	
	4	Bumblebees	Solitary bees	0.220	0.231 (-0.141-0.603)	-0.131 (-0.482-0.220)	0.173 (-0.222-0.568)	0.441 (0.143-0.739)	0.014 (-0.311-0.340)	-0.065 (-0.254-0.125)	
<b>D</b>	5	All pollinators	Bumblebees	0.105	0.203 (-0.188-0.594)	-0.139 (-0.444-0.165)	0.176 (-0.232-0.583)	0.194 (-0.149-0.537)	0.285 (-0.151-0.721)	-0.404 (-0.648-0.159)	
	<b>1</b>	<b>Bumblebees</b>	<b>All pollinators</b>	<b>0.105</b>	<b>0.042 (-0.269-0.353)</b>	<b>-0.007 (-0.305-0.291)</b>	<b>0.040 (-0.284-0.363)</b>	<b>0.284 (-0.222-0.791)</b>	<b>0.107 (-0.334-0.548)</b>	<b>0.178 (0.043-0.314)</b>	
	2	Bumblebees	Solitary bees	0.104	0.043 (-0.274-0.360)	-0.003 (-0.290-0.284)	0.042 (-0.287-0.371)	0.285 (-0.212-0.782)	0.101 (-0.252-0.454)	0.180 (-0.023-0.382)	
	3	Bumblebees	Bumblebees	0.100	0.039 (-0.283-0.360)	-0.072 (-0.321-0.178)	0.014 (-0.318-0.347)	0.340 (-0.212-0.891)	-0.094 (-0.491-0.303)	0.381 (0.141-0.621)	
	4	Bumblebees	Hoverflies	0.094	0.030 (-0.280-0.340)	-0.028 (-0.337-0.282)	0.021 (-0.309-0.351)	0.301 (-0.204-0.806)	0.035 (-0.297-0.367)	0.064 (-0.149-0.277)	
<b>E</b>	5	All pollinators	All pollinators	0.049	0.016 (-0.283-0.316)	0.146 (-0.074-0.366)	0.040 (-0.282-0.361)	0.159 (-0.664-0.983)	0.116 (-0.358-0.590)	0.264 (0.104-0.424)	
	<b>1</b>	<b>Solitary bees</b>	<b>Hoverflies</b>	<b>0.635</b>	<b>0.605 (0.373-0.837)</b>	<b>0.234 (0.020-0.448)</b>	<b>0.670 (0.462-0.877)</b>	<b>0.276 (-0.020-0.571)</b>	<b>0.283 (-0.015-0.581)</b>	<b>0.230 (-0.082-0.542)</b>	
	2	All pollinators	Hoverflies	0.584	0.628 (0.402-0.855)	0.284 (0.055-0.514)	0.670 (0.467-0.872)	0.145 (-0.196-0.486)	0.297 (-0.034-0.628)	0.343 (0.090-0.597)	
	3	Bumblebees	Hoverflies	0.580	0.658 (0.443-0.873)	-0.098 (-0.265-0.068)	0.670 (0.457-0.882)	-0.115 (-0.348-0.117)	0.353 (0.082-0.624)	0.072 (-0.183-0.327)	
	4	Hoverflies	Hoverflies	0.575	0.637 (0.358-0.917)	0.327 (0.081-0.574)	0.670 (0.460-0.879)	0.098 (-0.422-0.618)	0.315 (0.010-0.619)	0.328 (0.081-0.575)	
<b>F</b>	5	Hoverflies	Hoverflies	0.571	0.701 (0.465-0.936)	0.416 (0.096-0.736)	0.670 (0.452-0.887)	-0.075 (-0.356-0.207)	0.371 (0.068-0.674)	0.388 (0.220-0.556)	
	<b>1</b>	<b>Bumblebees</b>	<b>Hoverflies</b>	<b>0.240</b>	<b>0.434 (0.114-0.754)</b>	<b>-0.124 (-0.397-0.150)</b>	<b>0.411 (0.077-0.746)</b>	<b>0.183 (-0.100-0.467)</b>	<b>0.182 (-0.112-0.476)</b>	<b>0.074 (-0.246-0.395)</b>	
	2	Bumblebees	Bumblebees	0.239	0.445 (0.111-0.780)	-0.144 (-0.399-0.111)	0.407 (0.046-0.767)	0.269 (-0.034-0.571)	-0.201 (-0.493-0.091)	0.350 (0.110-0.590)	
3	All pollinators	Hoverflies	0.221	0.430 (0.101-0.759)	-0.142 (-0.381-0.096)	0.411 (0.079-0.744)	0.131 (-0.368-0.630)	0.134 (-0.194-0.463)	0.470 (0.279-0.661)		
4	Honeybees	Hoverflies	0.216	0.420 (0.101-0.739)	0.092 (-0.563-0.379)	0.411 (0.076-0.746)	-0.092 (-0.563-0.379)	0.211 (-0.102-0.525)	0.175 (-0.157-0.506)		
5	Solitary bees	Hoverflies	0.211	0.420 (0.090-0.750)	-0.123 (-0.46-0.101)	0.411 (0.081-0.742)	0.069 (-0.584-0.723)	0.166 (-0.174-0.507)	0.423 (0.227-0.618)		

Models are ranked on the total explained variance ( $R^2$ ), and the highest ranked model is in bold and illustrated in Fig. 2. All values are standardised effect sizes with 95% confidence intervals.



**Figure 1** Averaged effect sizes of the selected SEMs per crop line. Standardised effect sizes in black rectangles indicate how strongly a factor is related to another. The total effect size of plant quality (upper right rectangle) consists of the direct effect of plant quality, and the indirect effect through visitation rate on marketable seed yield. The total effect size of pollination (lower right rectangle) consists of the direct effects of visitation rate and species richness. Plant quality is measured as basal circumference (cm). Effects of visitation rate (pollinators/minute) and species richness (estimated number of species per field) are contributed by different functional groups, depending on crop line. The double-headed arrow between visitation rate and species richness is a modelled correlation. For visualisation purposes arrows with high effect sizes are made thicker. For simplicity, unexplained variance is not shown.

almost half of the top five models explaining marketable seed yield, and was included in the best model in four out of five lines (Table 1).

### Economic contribution

To illustrate the practical consequences of our findings, we expressed the relationships described by the best models per line in economic terms. Pollinator visitation rate showed consistent positive relations with estimated crop value in all lines (Fig. 3). Plant quality and species richness were positively related to crop value in only four lines. An improvement in plant quality from the median to the 75<sup>th</sup> percentile of our observed range represented an estimated \$18 007 ha<sup>-1</sup> increase in value. A similar improvement in pollinator visitation rates represented an estimated \$12 236 ha<sup>-1</sup> increase in value, and an additional \$4 937 ha<sup>-1</sup> for species richness of the functional group contributing most to marketable seed yield.

### DISCUSSION

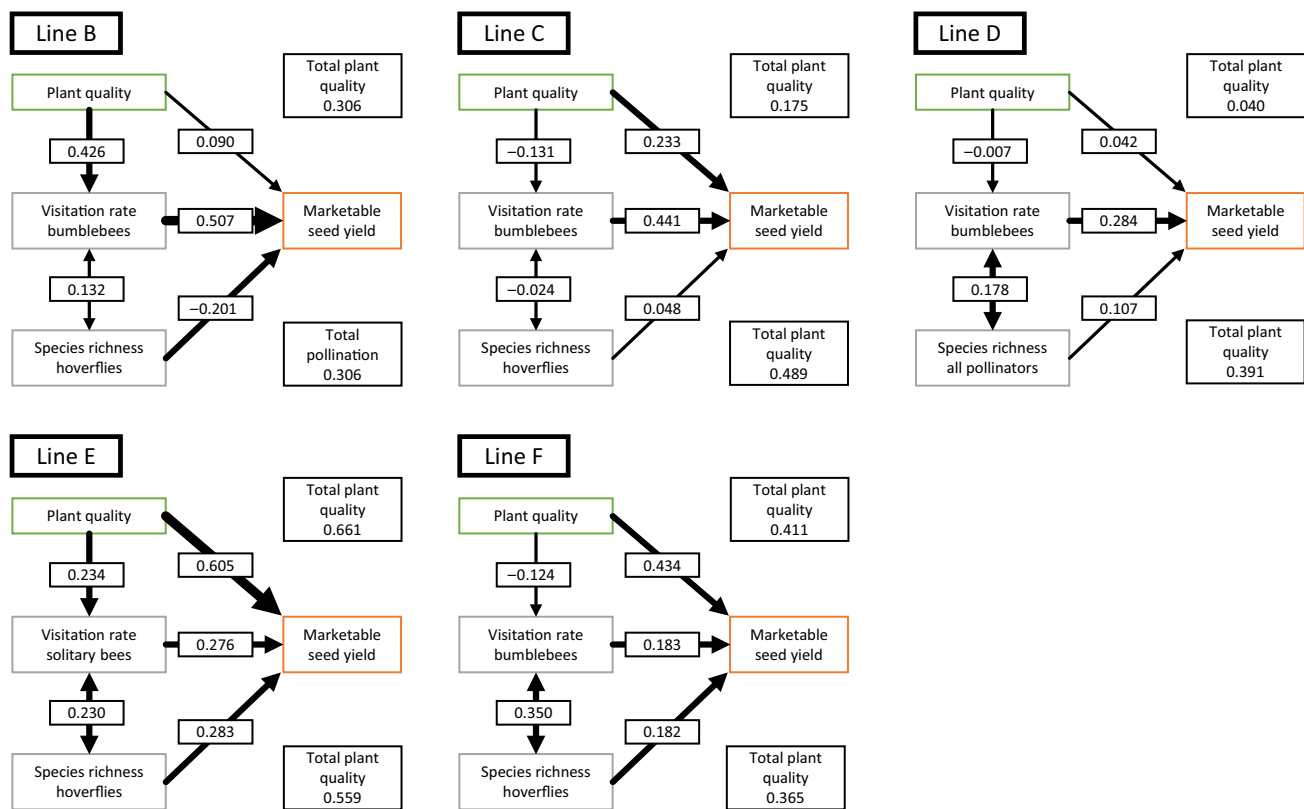
This study is the first endeavour comparing the relative contribution of pollination and regular agricultural management to crop yield, and shows that, although there were substantial differences between female lines, on average, insect pollination was at least as important as plant quality in the examined cropping system. Better agricultural management, through its effects on plant quality, did not invariably result in higher yields as we surprisingly found no relationship between plant quality and yield in one of the five examined crop lines. In contrast, higher visitation rate of wild pollinators invariably

resulted in higher marketable seed yield. Although our hybrid leek study system is fully dependent on insects to transfer pollen from the male to the female line, the important and systematic contribution of wild pollinators is still remarkable because our approach did not examine the effects of absence of pollinators (Garibaldi *et al.* 2018) but used the real-world variation in service-providing species. Our findings therefore suggest that wild pollinators are more consistently linked to marketable seed yield than plant quality. Since wild pollinators are rarely managed by growers this indicates that they are an undervalued agricultural input (IPBES 2016).

Interestingly, counter to findings from other studies (Klein *et al.* 2003; Garibaldi *et al.* 2013, 2016; Winfree *et al.* 2015) visitation rate of all pollinators combined did not relate well to marketable crop yield, suggesting that not all flower visits add up to enhance pollination and crop yield. Individual functional groups of pollinators did relate strongly to marketable crop yield, however which group was most effective differed between female lines. Visitation rate of bumblebees seem to play a key role in hybrid leek pollination in four out of five lines (Table 1). Bumblebees are known to be highly effective pollinators (Rader *et al.* 2009), and are among the most abundant pollinators in a wide variety of insect-pollinated crops (Kleijn *et al.* 2015). Nevertheless, crop yield was best explained by visitation rate of solitary bees in the fifth line (Line E; Fig. 2). Because in each field, the five lines were grown next to one another, the most likely explanation for this result is that this line was more attractive to solitary bees than the other lines, possibly because specific floral traits, such as nectar accessibility, better matched the requirements of this functional group (Garibaldi *et al.* 2015). Indeed, solitary bee visitation rate of line E was almost twice as high as bumblebee visitation rate although the opposite was the case in the neighbouring line B (Table S1), and that at the field level almost 3.5 times more bumblebees were observed than solitary bees (Table S2). The pollinator groups that provide the key services may therefore not only differ between crops (Garratt *et al.* 2014), but also between lines of the same crop.

Species richness effects were less pronounced and less consistent than visitation rate effects but were nevertheless important in two of the examined crop lines. Here species richness of hoverflies contributed substantially to marketable seed yield, and furthermore appeared in almost half of the models best explaining variation in crop yield (Table 1). Hoverflies are mainly active in the early morning (Herrera 1990) before most bees start visiting the crop and may therefore be the first pollinators to visit freshly opened flowers. This could have made them functionally complementary to the much more numerous wild bees (Frund *et al.* 2013). The negative relationship between hoverflies and seed yield in line B, not only for species richness but also for hoverfly visitation rate, suggests that hoverflies can also provide pollination disservices, but the exact mechanisms behind this remain unknown.

Our results suggest that for leek hybrid seed production two abundant bumblebees (*Bombus terrestris* and *B. lapidarius*) provide the majority of the pollination services, confirming previous observations that a small number of species provide the bulk of the services (Kleijn *et al.* 2015). This was not merely driven by abundance of species (Winfree *et al.* 2015)

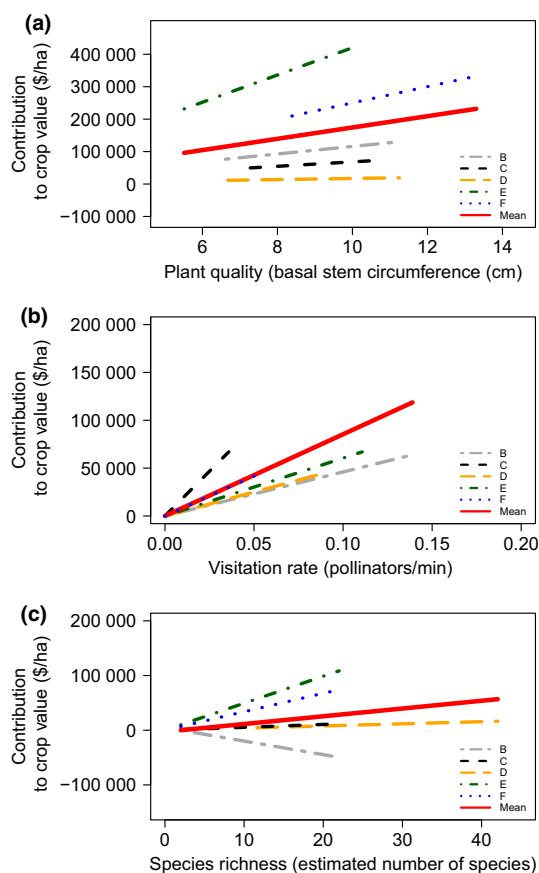


**Figure 2** Selected SEM for each female line based on highest explained variation out of 20 candidate models. Plant quality is measured as basal circumference (cm). Effects of visitation rate (pollinators/minute) and species richness (estimated number of species) are contributed by different functional groups, depending on crop line. Effect sizes are standardised and indicate how strongly factors are related to another. The total effect size of pollination (lower right rectangle) consists of the direct effects of visitation rate and species richness. Plant quality is measured as basal circumference (cm). Effects of visitation rate (pollinators/minute) and species richness (estimated number of species per field) are contributed by different functional groups, depending on crop line. The double-headed arrow between visitation rate and species richness is a modelled correlation. For visualisation purposes arrows with high effect sizes are made thicker. For simplicity, unexplained variance is not shown.

because the honeybee was the second most abundant flower visitor but hardly contributed to marketable seed yield. However, we found additional, sometimes important, contributions to crop yield of species richness of other functional groups of pollinators, and visitation rate of solitary bees was more closely related to crop yield of one line than the visitation rate of bumblebees (Fig. 2). Delivery of pollination services is therefore predominantly driven by abundance of key functional pollinator groups (Kleijn *et al.* 2015; Winfree *et al.* 2015), but, depending on the context, diversity and abundance of other pollinator groups may complement or largely replace the functional role of the dominant species. This indicates that a narrow focus of wild pollinator-enhancing management that is just targeting a few species of dominant crop pollinators will effectively enhance pollination under most conditions. However, this strategy may not suffice to provide resilient pollination services under all circumstances (Hudewenz *et al.* 2014; Marini *et al.* 2015) or at larger time (Riedinger *et al.* 2015) or spatial (Winfree *et al.* 2018) scales, as it can fail to enhance the species that can step in or supplement service provision when the dominant species are performing suboptimal, thus acting as insurance to farmers (Yachi & Loreau 1999).

All but one line showed only direct effects of agricultural management and pollination on marketable seed yield,

indicating that the contributions of conventional agricultural management and pollination to seed production were largely independent from each other (van Gils *et al.* 2016). This suggests that, in theory, insect pollination can replace external inputs such as fertilizer or pesticides to produce the same yield in a more sustainable way (Bommarco *et al.* 2013; Marini *et al.* 2015; Tamburini *et al.* 2017). However, a strategy that is probably more attractive to growers is to improve both insect pollination and agricultural management as this will result in the highest crop yields (Garibaldi *et al.* 2016). The main management strategy to enhance pollination in our study system is placement of honeybee hives (Rucker *et al.* 2012). In line with a growing body of evidence (Garibaldi *et al.* 2013), our study shows that managed honeybees cannot replace the pollination services provided by wild pollinators. Management aimed at increasing insect pollination should therefore be targeted at enhancing the abundance and diversity of the wild pollinator community. Three types of measures can be taken that are increasingly difficult for farmers to integrate into their farming systems. First and foremost, to avoid further loss of wild pollinators, the existing semi-natural habitats in agricultural landscapes should be conserved as pollinators depend critically on them for nesting, shelter and food outside the crop flowering season (Westrich 1996; Ricketts



**Figure 3** An illustration of the contribution of the measured factors to the estimated hybrid leek seed crop value. The contribution to the crop value along the observed 90% percentile of (a) plant quality (basal circumference (cm)), (b) visitation rate (pollinators/minute) and (c) species richness (estimated number of species), with average values of the other measured factors. The intercept for each line is set to zero. Economic value is calculated using the parameter estimates of the best SEM model and the observed 90% percentile measurements of each factor per line. The average slope of all female lines is superimposed with a solid red line.

*et al.* 2008; Garibaldi *et al.* 2011b; Dainese *et al.* 2017). Second, the quality of degraded semi-natural habitats in agricultural landscapes should be improved as this may be a cost-effective way to enhance wild pollinator communities (Morandin & Kremen 2013; M'Gonigle *et al.* 2015). Third, new wild pollinator habitats can be created by sowing diverse, native wildflower mixtures on field edges (Scheper *et al.* 2013; Blaauw & Isaacs 2014; Pywell *et al.* 2015; Sutter *et al.* 2017), which can even be targeted to particular groups of beneficial pollinators (Rundlof *et al.* 2014). Such practices are generally costly, which may prevent their adoption by single growers (Cong *et al.* 2014). However, our study shows that the economic benefits of increasing insect pollination in this hybrid-seed crop probably compensate for the costs of establishing wild flower strips (Blaauw & Isaacs 2014). This is likely the same for other insect-pollinated hybrid seed production crops, which could be an economic incentive for seed companies to take the lead in pollinator-enhancing management in agricultural landscapes that are poor in semi-natural habitats. Here, seed companies could sponsor the establishment of high

quality-pollinator habitat near pollinator-dependent seed crops, thus lowering the risks for growers and making it more attractive to invest in wild pollinators (Blaauw & Isaacs 2014). This way the cultivation of high-revenue seed crops could instigate the development of a more pollinator-friendly agricultural landscape, which in turn could have important positive side-effects on farmland biodiversity, the productivity of low-revenue insect-dependent crops (Isaacs *et al.* 2017) and the aesthetic value of agricultural landscapes (Breeze *et al.* 2015).

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## AUTHORSHIP

TPMF, JAS and DK conceived and designed the experimental setup. TPMF, NJ, TMB and IR collected data and identified the pollinators. TPMF performed analyses and wrote the initial manuscript. All co-authors contributed significantly to improving the manuscript.

## DATA ACCESSIBILITY

Data can be accessed in the Dryad Data Repository at <https://doi.org/10.5061/dryad.640v21f>.

## REFERENCES

- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J. *et al.* (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.*, 12, 8–17.
- Blaauw, B.R. & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.*, 51, 890–898.
- Blitzer, E.J., Gibbs, J., Park, M.G. & Danforth, B.N. (2016). Pollination services for apple are dependent on diverse wild bee communities. *Agric. Ecosyst. Environ.*, 221, 1–7.
- Bommarco, R., Kleijn, D. & Potts, S.G. (2013). Ecological intensification: harnessing ecosystem services for food security. *Trends Ecol. Evol.*, 28, 230–238.
- Breeze, T., Bailey, A., Potts, S. & Balcombe, K. (2015). A stated preference valuation of the non-market benefits of pollination services in the UK. *Ecol. Econ.*, 111, 76–85.
- Brewster, J.L. (2008). *Onions and Other Vegetable Alliums*. CABI, Oxfordshire, UK.
- Chao, A., Colwell, R.K., Lin, C.-W. & Gotelli, N.J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, 90, 1125–1133.



- Cong, R.-G., Smith, H.G., Olsson, O. & Brady, M. (2014). Managing ecosystem services for agriculture: will landscape-scale management pay? *Ecol. Econ.*, 99, 53–62.
- Dainese, M., Montecchiari, S., Sitzia, T., Sigura, M. & Marini, L. (2017). High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. *J. Appl. Ecol.*, 54, 380–388.
- Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R. & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Front. Ecol. Environ.*, 12, 212–217.
- Fijen, T.P.M. & Kleijn, D. (2017). How to efficiently obtain accurate estimates of flower visitation rates by pollinators. *Basic Appl. Ecol.*, 19, 11–18.
- Frund, J., Dormann, C.F., Holzschuh, A. & Tschardtke, T. (2013). Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, 94, 2042–2054.
- Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A. & Harder, L.D. (2011a). Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl Acad. Sci. USA*, 108, 5909–5914.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A. *et al.* (2011b). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.*, 14, 1062–1072.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. *et al.* (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, 339, 1608–1611.
- Garibaldi, L.A., Bartomeus, I., Bommarco, R., Klein, A.M., Cunningham, S.A., Aizen, M.A. *et al.* (2015). Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *J. Appl. Ecol.*, 52, 1436–1444.
- Garibaldi, L.A., Carvalheiro, L.G., Vaissiere, B.E., Gemmill-Herren, B., Hipolito, J., Freitas, B.M. *et al.* (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, 351, 388–391.
- Garibaldi, L.A., Andersson, G.K.S., Requier, F., Fijen, T.P.M., Hipólito, J., Kleijn, D. *et al.* (2018). Complementarity and synergisms among ecosystem services supporting crop yield. *Global Food Security*, 17, 38–47.
- Garratt, M.P., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R. *et al.* (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. *Biol. Conserv.*, 169, 128–135.
- van Gils, S., van der Putten, W.H., Kleijn, D. & Mori, A. (2016). Can above-ground ecosystem services compensate for reduced fertilizer input and soil organic matter in annual crops? *J. Appl. Ecol.*, 53, 1186–1194.
- Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, New York City, NY.
- Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589–596.
- Guarda, G., Padovan, S. & Delogu, G. (2004). Grain yield, nitrogen-use efficiency and baking quality of old and modern Italian bread-wheat cultivars grown at different nitrogen levels. *Eur. J. Agron.*, 21, 181–192.
- Hanes, S.P., Collum, K.K., Hoshida, A.K. & Asare, E. (2015). Grower perceptions of native pollinators and pollination strategies in the lowbush blueberry industry. *Renew. Agric. Food Syst.*, 30, 124–131.
- Herrera, C.M. (1990). Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering mediterranean shrub. *Oikos*, 58, 277–288.
- Hoehn, P., Tschardtke, T., Tyljanakis, J.M. & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. B*, 275, 2283–2291.
- Hudewenz, A., Pufal, G., Bogeholz, A.L. & Klein, A.M. (2014). Cross-pollination benefits differ among oilseed rape varieties. *J. Agric. Sci.*, 152, 770–778.
- IPBES (2016). The assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. (eds Potts, S., Imperatriz-Fonseca, V. & Ngo, H.). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, p. 552.
- Isaacs, R., Williams, N., Ellis, J., Pitts-Singer, T.L., Bommarco, R. & Vaughan, M. (2017). Integrated crop pollination: combining strategies to ensure stable and sustainable yields of pollination-dependent crops. *Basic Appl. Ecol.*, 22, 44–60.
- Jauker, F., Bondarenko, B., Becker, H.C. & Steffan-Dewenter, I. (2012). Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agric. For. Entomol.*, 14, 81–87.
- Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. *et al.* (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proc. R. Soc. B*, 281, 20132440.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R. *et al.* (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.*, 6, 7414.
- Klein, A.M., Steffan-Dewenter, I. & Tschardtke, T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. B*, 270, 955–961.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.* (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B*, 274, 303–313.
- Kremen, C., Williams, N.M. & Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. USA*, 99, 16812–16816.
- Kynetec (2017). *Sigma™ Seed Vegetable Crops – Harvest Year 2016*. Kynetec, Berks, UK.
- Major, D. (1980). Environmental effects on flowering. In: *Hybridization of Crop Plants* (eds Fehr, W., Hadley, H.). American Society of Agronomy–Crop Science Society of America, Madison, Wisconsin, pp. 1–15.
- Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindstrom, S.A.M., Zanetti, F., Mosca, G. *et al.* (2015). Crop management modifies the benefits of insect pollination in oilseed rape. *Agric. Ecosyst. Environ.*, 207, 61–66.
- M’Gonigle, L.K., Ponisio, L.C., Cutler, K. & Kremen, C. (2015). Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecol. Appl.*, 25, 1557–1565.
- Morandini, L.A. & Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol. Appl.*, 23, 829–839.
- Munyuli, T. (2011). Farmers’ perceptions of pollinators’ importance in coffee production in Uganda. *Agric. Sci.*, 2, 318.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345–353.
- Pywell, R.F., Heard, M.S., Woodcock, B.A., Hinsley, S., Ridding, L., Nowakowski, M. *et al.* (2015). Wildlife-friendly farming increases crop yield: evidence for ecological intensification. *Proc. R. Soc. B*, 282, 20151740.
- R Core Team (2018). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A., Newstrom-Lloyd, L.E., Walker, M.K. *et al.* (2009). Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J. Appl. Ecol.*, 46, 1080–1087.
- Rader, R., Edwards, W., Westcott, D.A., Cunningham, S.A. & Howlett, B.G. (2013). Diurnal effectiveness of pollination by bees and flies in agricultural Brassica rapa: implications for ecosystem resilience. *Basic Appl. Ecol.*, 14, 20–27.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R. *et al.* (2016). Non-bee insects are important contributors to global crop pollination. *Proc. Natl Acad. Sci. USA*, 113, 146–151.

- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A. *et al.* (2008). Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.*, 11, 499–515.
- Riedinger, V., Mitesser, O., Hovestadt, T., Steffan-Dewenter, I. & Holzschuh, A. (2015). Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology*, 96, 1351–1360.
- Rosseel, Y. (2011). *Lavaan: An R Package for Structural Equation Modeling and More Version 0.4-9 (BETA)*. Ghent University, Ghent.
- Rucker, R.R., Thurman, W.N. & Burgett, M. (2012). Honey bee pollination markets and the internalization of reciprocal benefits. *Am. J. Agric. Econ.*, 94, 956–977.
- Rundlof, M., Persson, A.S., Smith, H.G. & Bommarco, R. (2014). Late-season mass-flowering red clover increases bumble bee queen and male densities. *Biol. Conserv.*, 172, 138–145.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlof, M., Smith, H.G. *et al.* (2013). Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss—a meta-analysis. *Ecol. Lett.*, 16, 912–920.
- Schermelleh-Engel, K., Moosbrugger, H. & Müller, H. (2003). Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. *Methods Psychol. Res. Online*, 8, 23–74.
- Sørensen, J.N., Johansen, A.S. & Kaack, K. (1995). Marketable and nutritional quality of leeks as affected by water and nitrogen supply and plant age at Harvest. *J. Sci. Food Agric.*, 68, 367–373.
- Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G. & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *J. Appl. Ecol.*, 54, 1856–1864.
- Tamburini, G., Berti, A., Morari, F. & Marini, L. (2016). Degradation of soil fertility can cancel pollination benefits in sunflower. *Oecologia*, 180, 581–587.
- Tamburini, G., Lami, F. & Marini, L. (2017). Pollination benefits are maximized at intermediate nutrient levels. *Proc. R. Soc. B*, 284, DOI: 10.1098/rspb.2017.0729.
- Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011). Global food demand and the sustainable intensification of agriculture. *Proc. Natl Acad. Sci. USA*, 108, 20260–20264.
- Wagg, C., Bender, S.F., Widmer, F. & van der Heijden, M.G.A. (2014). Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proc. Natl Acad. Sci. USA*, 111, 5266–5270.
- Weston, R. & Gore, P.A. (2006). A brief guide to structural equation modeling. *Couns. Psychol.*, 34, 719–751.
- Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T. *et al.* (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.*, 78, 653–671.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In: *Linnean Society Symposium Series* (eds Matheson, A.). Academic Press Limited, London, UK, pp. 1–16.
- Williams, P.H., Brown, M.J., Carolan, J.C., An, J., Goulson, D., Aytekin, A.M. *et al.* (2012). Unveiling cryptic species of the bumblebee subgenus *Bombus* s. str. worldwide with COI barcodes (Hymenoptera: Apidae). *Syst. Biodivers.*, 10, 21–56.
- Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.*, 18, 626–635.
- Winfree, R., Reilly, J.R., Bartomeus, I., Cariveau, D.P., Williams, N.M. & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, 359, 791–793.
- Wright, H. (1980). Commercial hybrid seed production. In: *Hybridization of Crop Plants* (eds Fehr, W., Hadley, H.). American Society of Agronomy – Crop Science Society of America, Madison, Wisconsin, pp. 161–176.
- Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl Acad. Sci. USA*, 96, 1463–1468.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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