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Late flowering time enhances insect pollination of turnip rape

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Abstract

1. Ecological intensification has been proposed as a strategy to mitigate the impacts of conventional intensive land use on pollinators and insect pollination. However, research has concentrated on the effects of land management on pollinator abundance and diversity, while studies directly measuring pollination services are still lacking for many crops and regions.
2. This study examines the effects of landscape heterogeneity, pesticide use intensity and flowering time on insect pollination of turnip rape (*Brassica rapa* ssp. *oleifera*), a major oil crop at high latitudes. The field experiment included monitoring pollinator visits on turnip rape flowers and measuring yield in 34 spring-sown turnip rape fields in Southern Finland. The fields were situated in two landscape types that differed in the cover of arable land and represented independent gradients of pesticide use intensity and flowering time.
3. Based on flower visits and number of seeds per silique, turnip rape was best pollinated in fields with late flowering time. The result suggests a temporal mismatch between crop flowering and the availability of pollination service in early sown fields. The increase in flower visits during summer was steeper among fields with low than high pesticide use, possibly due to a faster colony growth of important bee pollinators.
4. Pollinator community in turnip rape fields was more diverse in heterogeneous landscapes with less arable land than in homogenous field-dominated landscapes, suggesting higher stability of pollination services in diverse landscapes.
5. Total yield per plant was positively related to pesticide use intensity. The relationship between insect pollination and total yield was weakened by high compensation capacity of turnip rape, the plants producing more flowers under poor pollination.
6. *Synthesis and applications.* Crop pollination can be enhanced by shifting sowing time to better match crop flowering to the peak availability of the most important pollinators.

Reduced pesticide use may also enhance pollination services but can lead to the total yield reduction due to pests. This highlights the need for pollinator-friendly pest control methods to maintain turnip rape yields while conserving pollination services.

Tiivistelmä (Finnish abstract)

1. Maatalouden ekologista tehostamista on esitetty strategiaksi, jonka avulla intensiivisen maankäytön kielteisiä vaikutuksia pölyttäjiin ja hyönteispölytykseen voidaan hillitä. Tutkimukset maankäytön vaikutuksista viljelykasvien hyönteispölytykseen kuitenkin puuttuvat yhä monilta viljelykasveilta ja alueilta.
2. Tämä tutkimus tarkasteli maiseman monimuotoisuuden, torjunta-aineiden käytön ja kukinta-ajan vaikutusta rypsin hyönteispölytykseen. Peltokokeessa seurattiin pölyttäjien vierailuja rypsin kukilla ja mitattiin satoa 34 kevätrypsipelloilla Uudellamaalla. Pellot sijaitsivat kahdessa maisematypissä, joista toinen oli peltovaltainen ja toinen monimuotoisempi ja vähemmän peltoa sisältävä. Lisäksi pellot erosivat toisistaan torjunta-aineiden käytön ja kukinta-ajan suhteen.
3. Pölyttäjien kukkavierailut ja siementen määrä per litu olivat korkeimmillaan myöhään kukkineilla rypsipelloilla, mikä kertoo hyvästä pölytyksestä. Tuloksen perusteella aikaisin kylvetyt rypsipellot saattavat kukkia liian aikaisin pölyttäjien saatavuuden näkökulmasta. Voimakkaimmin pölyttäjien määrä lisääntyi kesän aikana niiden peltojen joukossa, joilla ei käytetty torjunta-aineita. Mahdollinen selitys on, että tarhamehiläisten ja kimalaisten yhdyskunnat kasvoivat nopeimmin näiden peltojen läheisyydessä.
4. Pölyttäjien monimuotoisuus oli suurempi monimuotoisessa kuin peltovaltaisessa maisemassa, mikä parantaa pölytyspalvelun vakautta muuttuvissa olosuhteissa.

5. Kokonaissato per kasvi nousi torjunta-aineiden käytön lisääntyessä. Hyönteispölytyksen ja sadon välistä yhteyttä heikensi rypsin hyvä kompensatiokyky, jonka ansiosta heikosti pölyttyneet kasvit tuottivat enemmän kukkia.
6. *Yhteenveto ja sovellukset.* Viljelykasvin pölytystä voi parantaa säätämällä kylvöaikaa siten, että kasvin kukinta ajoittuu tärkeimpien pölyttäjien runsaahuippuun. Torjunta-aineiden käytön vähentäminen voi parantaa pölytystä mutta laskea samaan aikaan satoa tuholaisten ja rikkakasvien lisääntymisen takia. Pölyttäjäystävällisten kasvinsuojelukeinojen kehittäminen on tärkeää korkeiden rypsisatojen ja pölytyspalveluiden säilymisen kannalta.

Keywords

bees, ecological intensification, flower visitation, landscape heterogeneity, pesticide use, pollinators, syrphid flies, turnip rape

1 Introduction

Pollinator decline threatens biodiversity, ecosystems functioning and human well-being worldwide (Potts et al., 2016). Globally, over 75% of all food crops rely, at least partly, on animal pollination (Klein et al., 2007). Over the past 50 years, agriculture has become more dependent on insect pollination (Aizen, Garibaldi, Cunningham, & Klein, 2009), while yields of insect-pollinated crops have increased at a lower rate and become more variable than yields of wind-pollinated crops, suggesting increasing pollination deficits (Garibaldi, Aizen, Klein, Cunningham, & Harder, 2011).

Among the most important drivers of pollinator decline are habitat loss and degradation due to conventional agricultural intensification (Potts et al., 2016). The simplification of agricultural landscapes, loss of natural and semi-natural habitats, and herbicide use reduce floral and nesting resources of pollinators (Svensson, Lagerlof, & Svensson, 2000; Gabriel & Tscharntke, 2007; Baude et al., 2016). Pollinators also suffer from insecticides, which have both lethal and a broad range of sublethal impacts (Godfray et al., 2015; Pisa et al., 2015). Neonicotinoids, the most widely used group of insecticides worldwide (Wood & Goulson, 2017), have been reported to reduce wild bee populations (Goulson, 2015; Rundlöf et al., 2015; Woodcock et al., 2017; Arce et al., 2017) and crop pollination services provided by them (Stanley et al., 2015). The negative effect is emphasized in landscapes with low cover of natural and semi-natural habitats (Park, Blitzer, Gibbs, Losey, & Danforth, 2015), and scarce floral resources (Goulson, Nicholls, Botías, & Rotheray, 2015). In the European Union, outdoor use of three most widely used neonicotinoids (clothianidin, imidacloprid and thiamethoxam) has been restricted since 2013, and was completely banned recently (European Commission, 2018).

To protect pollinators and secure pollination services, researchers have suggested shifting to ecological intensification (Dicks et al., 2016; IPBES, 2016). The strategy involves actively managing

ecological functions such as insect pollination and biological pest control for highly productive agriculture (Bommarco, Kleijn, & Potts, 2013; Tittone, 2014). Many practices under ecological intensification, such as the establishment of fallows and wildflower strips, diversification of cropping systems, and reduction of pesticide use, contribute to mitigating pollinator declines (Kovács-Hostyánszki et al., 2017). However, more knowledge is needed on the level of pollinator diversity and abundance required for desired pollination services and high yields, and how this can be reached in different crops and regions (Dicks et al., 2016; Kovács-Hostyánszki et al., 2017).

An almost completely unstudied question is how flowering time affects crop pollination (but see Kőrösi et al., 2018; Pisanty, Afik, Wajnberg, Mandelik, & Diekötter, 2015). If the availability of main pollinators changes over summer, crop pollination could potentially be enhanced by adjusting crop flowering time. For annual crops, this can be done by shifting sowing date within the limits set by climatic conditions and crop growing times. The need for studying the method is emphasized by ongoing global climate change, which may induce phenological mismatches between crops and their pollinators (Kőrösi et al., 2018; Memmott, Craze, Waser, & Price, 2007).

Turnip rape (*Brassica rapa* ssp. *oleifera*) is grown as oil and protein crop in Northern Europe and Canada. In Finland, it covers 28,500 hectares, corresponding to 1.4% of total cultivated area (Natural Resources Institute Finland, 2018). By contrast to oilseed rape (*Brassica napus* ssp. *oleifera*), the world's major Brassica crop, turnip rape is almost self-sterile requiring cross-pollination by wind or animals to set seed (Williams, 1978; Korpela, 1988). The main pollinators are Hymenoptera, especially honeybees (*Apis mellifera*), and Diptera (Brunel, Mesquida, Renard, & Tanguy, 1994; Varis, 1995). In Finland, the long-term regional yields of turnip rape have decreased alongside with increasing use of neonicotinoid pesticides and decreasing complexity of agricultural landscapes, possibly due to disruption of pollination services (Hokkanen, Menzler-Hokkanen, & Keva, 2017).

The objective of this study was to examine the effects of landscape heterogeneity, pesticide use and flowering time on the insect pollination and yield of spring-sown turnip rape in boreal farmland. The study fields were situated in landscape types with two levels of heterogeneity, homogeneous and heterogeneous, and represented gradients of pesticide use intensity and flowering time. We hypothesized that turnip rape fields in heterogeneous landscapes, and with low pesticide use have high pollinator abundance and species richness, which enhance crop pollination and yield. Furthermore, we hypothesized that, due to the colony growth of social bees, the availability of turnip rape pollinators increases during summer, resulting in enhanced pollination and yield in late flowering fields.

2 Materials and methods

2.1 Study fields

The study was conducted in boreal farmland-forest mosaic landscapes of Southern Finland (60°9'–60°46'N, 23°49'–26°2'E) in the summer of 2017. A total of 34 turnip rape fields were selected from two landscape types differing in the percentage cover of arable land. A half of the fields were situated in homogenous landscapes with over 60% of arable land, and the other half in heterogeneous landscapes with less than 52% of arable land (Fig. 1, Table 1). Forest was the dominating uncultivated land use type (Table 1), and negatively correlated with arable land cover (Pearson's $r = -0.82$, $p < 0.001$). In boreal farmland, forests play a central role in modifying pollinator diversity by providing flower-rich edge habitats and shelter from wind, and by channeling pollinator movements (Öckinger, Lindborg, Sjödin, & Bommarco, 2012; Toivonen et al., 2017). The cover of arable land and other land use types was calculated for an area with a buffer of 500-m radius around the central point of the study site using ArcGIS 10.5.1 (Esri, 2017). Although many pollinators can forage over larger distances than 500 m, they usually prefer nearby resources when available

(Couvillon et al., 2015; Redhead et al., 2016). The minimum distance between the fields was 1 km. Data on land use were derived from the CORINE Land Cover 2012 database (Finnish Environment Institute, 2014). In addition, nine crop types, including turnip rape and oilseed rape, faba bean, red clover, buckwheat, spring cereals, winter cereals, cultivated grassland, perennial fallow and bare fallow were recorded during fieldwork. Shannon's diversity index (H') for land use diversity was calculated based on CORINE's level 3 land cover types (Finnish Environment Institute, 2014), and for crop diversity based on the relative cover of the recorded crop types (Table 1).

Information on the farming methods on the turnip rape fields was gathered through farmer interviews (Table 2). In both landscape types, there was a considerable variation among fields in pesticide use and the starting date of flowering (Table 2). The latter was strongly related to sowing date (see Table S1 in Supporting Information). The number of pesticide applications in a field, including seed treatments and field sprayings with insecticides, herbicides and fungicides was used as a proxy for pesticide use intensity (Dormann et al., 2007; Filippi-Codaccioni, Devictor, Bas, Clobert, & Julliard, 2010). Despite restrictions on the use of neonicotinoid insecticides in the European Union, turnip rape seeds treated with neonicotinoids are used in Finland based on temporary permissions (Tukes, 2016). Pesticide use intensity and flowering time were not correlated (Table S1), and they did not differ between the landscape types (Table 2).

The fields were sown with seven turnip rape varieties (Table 2), which did not differ in flowering time (ANOVA, $df = 6$, $F = 1.02$, $p = 0.43$) or pesticide use intensity (ANOVA, $df = 6$, $F = 0.76$, $p = 0.61$). 35% of the fields had honey bee hives within the surrounding 500-m buffer. The number of honey bee hives per turnip rape hectare did not differ between the landscape types (Table 2) and was not correlated with pesticide use intensity or flowering time (Table S1).

Figure 1. Locations of the 34 study fields representing two landscape types (characterized in Table 1) in Southern Finland.

Table 1. Comparison of the two landscape types. Percentage cover of arable land and forests were calculated within 500-m buffer. Distance to forest was measured from the sampling plot closest to forest. Shannon's diversity index (H') for land use diversity is based on CORINE's level 3 land cover types (Finnish Environment Institute, 2014), and for crop diversity on the relative cover of crop types.

	Landscape types		Welch two-sample t-test		
	Homogenous ($n=17$)	Heterogeneous ($n=17$)	t	df	p
Land use in 500-m buffer	mean [min, max]	mean [min, max]			
Arable land (%)	75 [60, 96]	32 [9, 51]	-10.61	31.27	<0.001
Turnip rape and oilseed rape (%)	19 [3, 52]	9 [2, 22]	-2.83	22.07	<0.01
Other insect-pollinated crops (%)	1 [0, 9]	1 [0, 8]	-0.85	30.29	ns
Cereals (%)	44 [15, 68]	18 [0, 38]	-5.39	28.36	<0.001
Perennial grasslands (%)*	12 [0, 44]	5 [0, 32]	-2.02	27.05	ns
Forest (%)	11 [0, 35]	48 [2, 80]	5.82	22.19	<0.001
Distance to forest (m)	203 [79, 421]	21 [7, 71]	-8.71	17.30	<0.001
Land use diversity (H)	0.60 [0.14, 1.19]	1.00 [0.68, 1.36]	4.42	30.96	<0.001
Crop diversity (H)	0.88 [0.47, 1.18]	0.82 [0.46, 1.30]	1.76	31.91	ns

* Perennial grasslands included sown cultivated grasslands and perennial fallows.

Table 2. Comparison of key farming characteristics of the studied turnip rape fields in the two landscape types. ‘Pesticide use intensity’ is the total number of pesticide applications in a field, including seed treatments and field sprayings with insecticides, herbicides and fungicides.

Field characteristics	Landscape types		Welch two-sample t-test		
	Homogenous (n = 17)	Heterogeneous (n = 17)	df	t	p
Mean [min, max]					
Area (ha)	9.9 [2.1, 33.3]	4.7 [0.8, 10.5]	19.01	-2.16	<0.05
Sowing date	21.5. [10.5., 17.6.]	21.5. [10.5., 28.5.]	26.33	-0.09	ns
Starting date of flowering	5.7. [26.6., 22.7.]	2.7. [28.6., 15.7.]	31.29	1.17	ns
Honey bee hives / ha of turnip rape	0.32 [0.00, 2.63]	0.39 [0.00, 2.64]	31.57	0.26	ns
Pesticide use intensity	2.59 [0, 5]	2.41 [0, 5]	31.53	-0.32	ns
Number of fields with					
Seed treatment with neonicotinoids	15	14			
Insecticide spraying	10	10			
Herbicide spraying	9	10			
Fungicide spraying	4	5			
Organic farming	2	1			
Reduced tillage	0	3			
Turnip rape varieties (number of fields)	Cordelia(5), Juliet(7), Petita(5)	Agat(1), Apollo(1), Aurea(2), Cordelia(5), Petita(6), Synthia(2)			

2.2 Monitoring of flower visits

In the study fields, pollinators were monitored in four 2 x 2 m squares placed at 5 and 20 m distances from an open field edge (i.e. field edge not bordered by forest). At both distances from the edge, two squares were placed in parallel, 50 m from each other. In homogenous landscapes, the field edge that situated farthest from forest was selected, whereas, in heterogeneous landscapes, the open edge closest to forest was chosen. The systematic selection of the edges enabled to strengthen the differences between the landscape types in arable land cover while avoiding selection bias. The pollinator monitoring squares were marked with bamboo sticks. Three times during flowering, every square was monitored for 5 minutes, and all pollinators visiting turnip rape flowers and the number of visits where the insect touched the reproductive parts of the flower were

recorded. Bumblebees and butterflies were identified to species, except for *Bombus lucorum* -group (*B. lucorum*, *B. terrestris*, *B. cryptarum* and *B. magnus*) that was treated as a one species. Solitary bees were recorded as a group. Syrphid flies were identified to subfamilies Syrphinae and Eristalinae. Pollinator monitoring was carried out between 9 a.m. and 6 p.m., in weather conditions when pollinator insects were active. Minimum temperature was 15 °C in sunny or partly cloudy and 17 °C in cloudy weather. Maximum wind speed was 5 on the Beaufort scale. Mean wind speed of repeated measurements on an individual field ranged between 1.3 and 3.3.

2.3 Measuring yield

Yield was measured from eight open-pollinated and eight control plants per field. Before flowering, two control plants at two meter distance from each pollinator monitoring square were covered with a light fabric bag (45 × 75 cm, white polyester voile, mesh size 0.32 × 0.32 mm) supported by a 1-m-long bamboo stick. The bag excluded pollinator visits but allowed cross-pollination by wind within the bag. After flowering, the bags were removed. When the crop was ripe, the control plants were collected. In addition, two open-pollinated plants were collected next to the marking stick of each pollinator monitoring square. Racemes per plant, siliques per raceme, and seeds per five lowest siliques of the main raceme were counted, after which the plants were dried at room temperature. Dry plants were harvested by hand, and seeds were weighed. To estimate weight per 100 seeds, the total seed weight per plant was divided by the number of siliques per plant and seeds per silique, and multiplied by 100.

2.4 Statistical analyses

An information theoretic approach was used to analyze the effects of landscape type, pesticide use intensity and flowering time on flower visits, pollinator species richness and yield. Since the

explanatory variables got their values at field level, response variables were also aggregated by fields. Thus, the response variables were the total number of flower visits and pollinator species across four monitoring squares and three monitoring times in each field, average number of seeds per silique, siliques per raceme and racemes per plant across the monitoring squares, and average weight of 100 seeds and total seed yield per plant across the monitoring squares. For each response variable, a total of nine competing models were constructed by including one to three of the following variables as predictors: landscape type, pesticide use intensity, flowering time and two-way interactions among them. Landscape type was a categorical variable with two levels, homogenous and heterogeneous, while pesticide use intensity and flowering time were treated as continuous.

Model types differed between the response variables: Generalized linear models (GLM) with Poisson errors were used to model the number of flower visits and pollinator species richness. For flower visits, quasi-likelihood estimation was used in the models because of overdispersion. For siliques per raceme, racemes per plant and weight per 100 seeds, linear models (LM) were applied. For seeds per silique and total yield per plant, generalized least squares models (GLS) with normal errors and a spatial Gaussian correlation structure were selected, because the residuals of LMs were spatially autocorrelated. Spatial autocorrelation was tested by Moran's I test using the function `moran.test()` of the R package `spdep` (Bivand & Piras, 2015). The Akaike Information Criterion corrected for small sample sizes (AICc) was used to compare the candidate models. For flower visits with quasi-Poisson models, AICc was replaced by the quasi-Akaike Information Criterion for small samples (QAICc). Model averaging was performed over all the models with $\Delta(Q)AICc < 6$ by weighting parameter coefficients according to their model probabilities (Akaike weights, w_i) (Burnham & Andersson, 2002). The R package `MuMIn` (Barton, 2018) was applied for model selection and model averaging.

In addition, the direct effects of flower visits and pollinator species richness on yield components and total yield per plant were analyzed with LMs, unless the residuals of the models were spatially autocorrelated, in which case GLS models with a spatial Gaussian correlation structure were selected. To examine the differences in yield components and total yield between open-pollinated plants and control plants with pollinator exclusion, linear mixed models (LMM) with field as a random factor were applied.

All analyses were conducted both with and without the latest flowering field with exceptionally high number of flower visits. The results of the analyses without the latest flowering field were included in Supplementary materials and reported in the main text if statistically significant explanatory variables differed from those identified in the analysis where all fields were included.

Models were fitted using the functions `glm()` and `lm()` of the R package `stats` (R Core Team, 2017), `gls()` of the package `nlme` (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2017) and `lmer()` of the package `lme4` (Bates, Maechler, Bolker, & Walker, 2015). All statistical analyses were run using R 3.4.1.

3 Results

A total of 4674 flower visits by 744 pollinator individuals were recorded. The pollinators represented 21 species or groups (Table S2). Managed honeybees made 72% of all flower visits and were present in 94% of the fields. The most frequent wild pollinators were bumblebees, with 16% of the flower visits.

3.1 Effects of landscape type, pesticide use and flowering time on insect pollination and yield

The number of flower visits was best explained by the flowering time and the interaction between flowering time and pesticide use intensity (Table 3, Table S3). Flower visits increased during flowering season, and the increase was strongest in fields with low pesticide use (Fig. 2a). When the latest flowering field was excluded from the analysis, the interactive effect of flowering time and pesticide use intensity was lost, while the effect of flowering time remained (Table S4).

Landscape type and flowering time explained pollinator species richness (Table 3, Table S3). Species richness was higher in heterogeneous than homogenous landscapes, and in late than early flowering fields (Fig. 2b). When the latest flowering field was excluded, the landscape type effect was lost, while the effect of flowering time remained (Table S4).

Flowering time also predicted the number of seeds per silique (Table 3, Table S3), with higher seed number in late than early flowering fields (Fig. 2c). The other yield components were not significantly explained by any of the predictors (Table S3, Table 3). Total seed yield per plant was significantly explained by pesticide use intensity (Table 3, Table S3), with increasing yield when pesticide use increased (Fig. 2d). When the latest flowering field was excluded, none of the yield variables responded statistically significantly to the predictors (Table S4).

Figure 2. Turnip rape pollination and yield in relation to the best explanatory variables in model averaging (Table 3): a) Total number of flower visits per field in relation to flowering time and pesticide use, b) pollinator species richness in relation to flowering time and landscape type, c) the number of seeds per silique in relation to the starting date of flowering, and d) yield per plant in relation to pesticide use. The contour plot (a) and the lines in the scatterplots (b–d) depict predicted values based on respective models. Due to overlapping data points, the number of dots in the plots is smaller than the number of study fields.

Table 3. Results of model averaging explaining the number of flower visits and pollinator species richness, yield components and total yield per plant. Model averaged parameter estimates were calculated from a confidence set of models including all models with a $\Delta(Q)AICc < 6$ (Table S3). Bolded terms have a 95% confidence interval (CI) that do not include zero.

Response variable	Model type	Parameter	Estimate	SE	Lower CI	Upper CI
Flower visits	GLM quasi-Poisson	(Intercept)	3.52	0.50	2.52	4.53
		Homogenous landscape ^a	-0.14	0.50	-1.16	0.87
		Pesticide use	0.23	0.29	-0.34	0.81
		Flowering time	0.12	0.03	0.07	0.18
		Homogenous landscape ^a : Flowering time	0.03	0.05	-0.07	0.14
		Pesticide use: Flowering time	-0.03	0.02	-0.07	-0.00
Pollinator species richness	GLM Poisson	(Intercept)	1.33	0.19	0.94	1.73
		Homogenous landscape^a	-0.40	0.23	-0.85	-0.02
		Flowering time	0.04	0.01	0.01	0.07
		Homogenous landscape ^a : Flowering time	0.00	0.01	-0.05	0.06
Seeds per silique	GLS	(Intercept)	9.64	1.72	6.13	13.15
		Homogenous landscape ^a	1.01	1.74	-2.55	4.56
		Pesticide use	0.25	0.63	-1.04	1.53
		Flowering time	0.37	0.15	0.07	0.66
		Homogenous landscape ^a : Flowering time	-0.05	0.29	-0.64	0.53
		Pesticide use: Flowering time	-0.03	0.08	-0.20	0.14
Siliques per raceme	LM	(Intercept)	12.10	1.43	9.22	14.99
		Homogenous landscape ^a	-0.27	1.12	-4.37	2.85
		Pesticide use	-0.05	0.36	-1.26	1.02
		Flowering time	-0.10	0.12	-0.41	0.11
		Homogenous landscape ^a : Pesticide use	0.03	0.22	-0.54	2.62
		Homogenous landscape ^a : Flowering time	0.01	0.07	-0.23	0.69
		Pesticide use: Flowering time	0.00	0.02	-0.21	0.06
Racemes per plant	LM	(Intercept)	5.01	1.11	2.77	7.24
		Homogenous landscape ^a	0.07	0.67	-2.23	2.68
		Pesticide use	0.33	0.35	-0.29	1.12
		Flowering time	-0.04	0.07	-0.27	0.08
		Homogenous landscape ^a : Pesticide use	0.04	0.20	-0.45	1.67
		Pesticide use: Flowering time	0.00	0.02	-0.04	0.14
Weight per 100 seeds	LM	(Intercept)	0.25	0.04	0.16	0.34
		Homogenous landscape ^a	0.00	0.04	-0.12	0.13
		Pesticide use	0.01	0.01	-0.02	0.04
		Flowering time	0.00	0.00	-0.01	0.01
		Homogenous landscape ^a : Pesticide use	0.00	0.01	-0.09	0.01
		Homogenous landscape ^a : Flowering time	0.00	0.00	-0.02	0.01
		Pesticide use: Flowering time	0.00	0.00	-0.00	0.01
Yield per plant	GLS	(Intercept)	1.22	0.34	0.53	1.91
		Homogenous landscape ^a	-0.01	0.15	-0.78	0.65
		Pesticide use	0.24	0.12	0.00	0.47

Flowering time	0.00	0.02	-0.08	0.05
Homogenous landscape ^a : Pesticide use	0.00	0.04	-0.33	0.45
Pesticide use: Flowering time	0.00	0.01	-0.02	0.05

^a As compared to heterogeneous landscape

3.2 Direct effects of insect pollination on yield

The number of seeds per silique increased, and racemes per plant decreased with increasing number of flower visits (Table 4, Figure 3). When the latest flowering field was excluded from the analyses, the effect on racemes was lost, while the effect on seeds per silique remained (Table S5). The other yield components and total yield per plant were not affected by flower visits (Table 4). Pollinator species richness did not affect any yield components (Table 4).

Control plants with pollinator exclusion produced 60% less yield than open-pollinated plants (Table 5). Seeds per silique, siliques per raceme and total seed weight were higher on open-pollinated plants, whereas enclosed plants had higher number of racemes (Table 5, Table S6).

Table 4. Effects of flower visits and pollinator species richness on yield components and total yield per plant.

Yield component	Model type	Flower visits				Pollinator species richness			
		Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Seeds per silique	GLS	0.011	0.004	2.940	<0.01	0.575	0.341	1.690	ns
Siliques per raceme	LM	-0.001	0.003	-0.485	ns	-0.210	0.260	-0.805	ns
Racemes per plant	LM	-0.004	0.002	-2.147	<0.05	-0.327	0.176	-1.859	ns
Weight (g) per 100 seeds	LM	-0.002	0.002	-1.002	ns	-0.011	0.038	-0.303	ns
Yield (g) per plant	GLS	-0.001	0.001	-0.977	ns	-0.059	0.069	-0.842	ns

Figure 3. Seeds per silique (a) and racemes per plant (b) in relation to the total number of flower visits per field. The lines depict predicted values based on the linear models.

Table 5. Comparison of the measured yield components and total yield between open-pollinated and bagged control plants.

Yield component	Model type	Open pollination		Pollinator exclusion		Estimate ^a	SE	<i>t</i>	<i>p</i>
		Mean	SD	Mean	SD				
Seeds per silique	LMM	12.74	4.78	5.14	2.32	-7.60	0.75	-10.15	<0.001
Siliques per raceme	LMM	11.02	3.44	7.24	2.30	-3.78	0.63	-5.97	<0.001
Racemes per plant	LMM	5.70	2.42	6.78	2.91	1.08	0.37	2.90	<0.01
Weight (g) per 100 seeds	LMM	0.24	0.11	0.32	0.28	0.08	0.05	1.66	ns
Yield (g) per plant	LMM	1.77	0.92	0.69	0.57	-1.08	0.14	-7.61	<0.001

^a Pollinator exclusion compared to open pollination

4 Discussion

Increasing pollinator visitation over the flowering period, and the associated increase in the number of seeds per silique showed that turnip rape was best pollinated in late flowering fields. The colonies of the most important pollinators, honeybees and bumblebees, probably grew in July (Westphal, Steffan-Dewenter, & Tschardtke, 2009; Ketola et al., 2015), resulting in increasing pollinator availability. Another explanation could be scarcity of floral resources in late summer, which would make turnip rape more attractive to pollinators (Heinrich, 1979). However, changes in the availability of wild flowers did not support this explanation, since flower abundance in the margins of the study fields increased towards the end of the turnip rape flowering season (Appendix S1). Analyzing changes in the availability of alternative crop resources for pollinators was not possible due to lack of data.

The phenological overlap with pollinators is crucial for any insect-pollinated plant (Memmott, Craze, Waser, & Price, 2007), but the effects of flowering time on crop pollination have received little attention in research (but see Kőrösi et al., 2018; Pisanty, Afik, Wajnberg, Mandelik, & Diekötter, 2015). To our knowledge, this is the first study suggesting that crop pollination could be enhanced by shifting sowing time to better match crop flowering to the availability of the most important pollinators. A farmer's decision when to sow is usually driven by local weather and soil conditions, availability of farm machinery and workload (Kaukoranta & Hakala, 2008). Climate change advances the timing of spring crop sowing at high latitudes, although not always at the same pace as the start of the thermal growing season (ibid.). This may affect crop-pollinator interactions, similarly to those for wild plants and pollinators (Memmott, Craze, Waser, & Price, 2007; Petanidou et al., 2014). Shifting sowing date is also known as a cultural pest management strategy (Knodel, Olson, Hanson, & Henson, 2008; Lundin, Myrbeck, & Bommarco, 2018). A recent study proposed early sowing as a potential method to reduce flea beetle (*Phyllotreta* spp.) damage in spring oilseed rape (Lundin, Myrbeck, & Bommarco, 2018). Early sowing also reduces the risk of yield losses due to late crop maturation. Trade-offs between different strategies should be studied to optimize the yield.

377

378 Faster increase of flower visits in fields with low pesticide use is consistent with previous findings on
379 the negative effects of pesticides on crop pollination services (Stanley et al., 2015). Recent studies
380 have found reduced colony growth and reproductive success of bees with exposure to neonicotinoid
381 insecticides (Goulson, 2015; Rundlöf et al., 2015, Arce et al., 2017; Woodcock et al., 2017). Besides
382 neonicotinoids, flower-visiting insects are routinely exposed to other insecticides, fungicides and
383 herbicides, of which single and combined effects in field conditions are largely unknown (Botías,
384 David, Hill, & Goulson, 2017; Tosi, Costa, Vesco, Quaglia, & Guido, 2018). Though not toxic to
385 pollinators, fungicides may weaken their resistance to pathogens (Pettis et al., 2013) and cause
386 synergistic mortality with insecticides (Raimets et al., 2018). Herbicides harm pollinators indirectly by
387 reducing diversity of their food resources (Goulson, Nicholls, Botías, & Rotheray, 2015). Reducing
388 pesticide use without negative effects on crop productivity is possible in some production systems,
389 especially if pesticide use is currently high (Lechenet, Dessaint, Py, Makowski, & Munier-Jolain,
390 2017). In our study, the increase in total yield per plant with increasing pesticide use suggests that
391 ecological intensification of turnip rape production requires introduction of enhanced non-chemical
392 control methods for pests and weeds.

393

394 Pollinator species richness was higher in heterogeneous than homogenous landscapes, which is
395 consistent with previous studies showing the dependency of pollinator diversity on natural and
396 semi-natural habitats in agricultural landscapes (Ricketts et al., 2008; Garibaldi et al., 2011;
397 Nicholson, Koh, Richardson, Beauchemin, & Ricketts, 2017). High pollinator diversity has been shown
398 to enhance the stability of pollination services in varying environmental conditions (Blüthgen &
399 Klein, 2011; Brittain, Kremen, & Klein, 2013), and in absence of honey bees (Winfree, Williams,
400 Dushoff, & Kremen, 2007; Breeze et al., 2014). In our study, pollinator species richness did not
401 explain seed production of turnip rape. Thus, variation in pollination services was probably mainly
402 driven by differences in the abundance of common species, similarly to Genung et al. (2017).

403

404 The effects of pesticide use and landscape type on insect pollination and yield lost their statistical
405 significance, though the patterns remained unchanged, when one field was excluded from the
406 analysis. More field studies, preferably under controlled conditions, are needed to confirm how
407 insect pollination of turnip rape is affected by pesticide use and landscape structure, and how
408 flowering time influences the effects.

409

410 Although the number of seeds per silique increased with increasing number of flower visits, total
411 yield per plant was not affected. This reveals that other factors than pollination, such as pest
412 pressure or nutrient availability had stronger effects on yield. Since information on pest and weed
413 abundance, soil characteristics and fertilization was not collected in the study, the main factor
414 limiting yield cannot be confirmed. Conventional management for high yields may conflict with
415 safeguarding pollination (Gagic et al., 2017): Pesticides reduce pest pressure, but simultaneously
416 impede pollination, and early sown plants, yet poorly pollinated, take advantage of the longer
417 growing season.

418

419 The relationship between insect pollination and total yield is further weakened by the high capacity
420 of oilseed Brassicas to compensate for losses early in the season by producing more racemes and
421 flowers, or by allocating resources into heavier seeds (Williams & Free, 1979; McGregor, 1981; Zou
422 et al., 2017). The opposite effects of flower visits on the number of seeds per silique and racemes
423 per plant suggest that yield compensation occurred in our study. The yield compensation capacity
424 may buffer turnip rape production against the effects of pollinator shortage. However, it does not
425 prevent yield losses, when pollination sinks under a critical level, as was shown with the pollinator
426 exclusion bags, where few flowers managed to develop siliques. In addition, good pollination
427 enhanced resource use efficiency, since well-pollinated plants grew fewer racemes to reach the yield
428 equal to that of poorly pollinated plants. Good insect pollination thus has potential to help reducing

dependency on external production inputs such as chemical fertilizers in resource efficient cropping systems (Marini et al., 2015).

5 Conclusions

Shifting sowing time to increase the temporal match between crop flowering and the peak availability of the most important pollinators holds promise as a method to enhance pollination. Reduced pesticide use may also benefit crop pollination, but can result in the total yield reduction due to pests and weeds. Thus, ecological intensification of turnip rape production, which maintains or increases yield while conserving pollination services, requires the replacement of chemical pesticides with pollinator-friendly pest control methods. Understanding the ecological interdependencies between agricultural practices, ecosystem services and yield in different crops and regions is needed to find ways to reduce environmental degradation and to sustain agricultural production in long-term.

Authors' contributions

All authors conceived the ideas and designed methodology. MT, HR and JT collected the data. MT analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data available via the KNB Data Repository <https://doi.org/10.5063/F1445JRF> (Toivonen, Herzon, Rajanen, Toikkanen, & Kuussaari, 2019).

References

Aizen, M. A., Garibaldi, L. A., Cunningham, S. A., & Klein, A. M. (2009). How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, 103, 1579–1588. doi: 10.1093/aob/mcp076

Arce, A. N., David, T. I., Randall, E. L., Rodrigues, A. R., Colgan, T. J., Wurm, Y., & Gill, R.J. (2017). Impact of controlled neonicotinoid exposure on bumblebees in a realistic field setting. *Journal of Applied Ecology*, 54, 1199–1208. doi: 10.1111/1365-2664.12792

Barton, K. (2018). MuMIn: Multi-Model Inference. R package version 1.40.4.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48. doi: 10.18637/jss.v067.i01.

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespi, M. A. K., ... Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530, 85–88. doi: 10.1038/nature16532

480

481 Bivand, R., & Piras, G. (2015). Comparing Implementations of Estimation Methods for Spatial
482 Econometrics. *Journal of Statistical Software*, 63, 1–36. doi: 10.18637/jss.v063.i18

483

484 Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: the role of
485 biodiversity in plant-pollinator interactions. *Basic and Applied Ecology*, 12, 282–291. doi:
486 10.1016/j.baae.2010.11.001

487

488 Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: harnessing ecosystem
489 services for food security. *Trends in Ecology and Evolution*, 28, 230–238. doi:
490 10.1016/j.tree.2012.10.012

491

492 Botías, C., David, A., Hill, E. M., & Goulson, D. (2017). Quantifying exposure of wild bumblebees to
493 mixtures of agrochemicals in agricultural and urban landscapes. *Environmental Pollution*, 222, 73–
494 82. doi: 10.1016/j.envpol.2017.01.001

495

496 Breeze, T. D., Vaissière, B. E., Bommarco, R., Petanidou, T., Seraphides, N., Kozák, L., ... Potts, S. G.
497 (2014). Agricultural policies exacerbate honeybee pollination service supply-demand mismatches
498 across Europe. *PLOS ONE*, 9, e82996. doi: 10.1371/journal.pone.0082996

499

500 Brittain, C., Kremen, C. & Klein, A. (2013). Biodiversity buffers pollination from changes in
501 environmental conditions. *Global Change Biology*, 19, 540–547. doi: 10.1111/gcb.12043

502

503 Brunel, E., Mesquida, J., Renard, M., & Tanguy, X. (1994). Répartition de l'entomofaune pollinisatrice
504 sur des fleurs de colza (*Brassica napus* L) et de navette (*Brassica campestris* L): incidence du
505 caractère apétale de la navette. *Apidologie*, 25, 12–20. doi: 10.1051/apido:19940102

506

507 Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodal inference: a practical
508 information-theoretic approach (2nd ed.). Berlin, Germany: Springer. doi: 10.1007/b97636

509

510 Couvillon, M., J., Riddell Pearce, F. C., Accleton, C., Fensome, K. A., Quah, S. K. L., Taylor, E. L., &
511 Ratnieks, F. L. W. (2015). Honey bee foraging distance depends on month and forage type.

512 *Apidologie*, 46, 61–70. doi: 10.1007/s13592-014-0302-5

513

514 Dicks, L., Viana, B., Bommarco, R., Brosi, B., Arizmendi, M., Cunningham, S., ... Potts, S. G. (2016). Ten
515 policies for pollinators. *Science*, 354, 975–976. doi: 10.1126/science.aai9226

516

517 Dormann, C. F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., De Blust, G., ... Zobel, M. (2007).
518 Effects of landscape structure and land-use intensity on similarity of plant and animal communities.

519 *Global Ecology and Biogeography*, 16, 774–787. doi: 10.1111/j.1466-8238.2007.00344.x.

520

521 Esri (2017). ArcGIS Desktop: Release 10.5.1. Redlands, CA: Environmental Systems Research
522 Institute.

523

524 European Commission (2018). Protecting bees: EU set to completely ban outdoor use of pesticides
525 harmful to bees. European Commission Daily News 27 / 04 / 2018. [http://europa.eu/rapid/press-](http://europa.eu/rapid/press-release_MEX-18-3583_en.htm)
526 [release_MEX-18-3583_en.htm](http://europa.eu/rapid/press-release_MEX-18-3583_en.htm) Last accessed: 15.1.2019

527

528 Filippi-Codaccioni, O., Devictor, V., Bas, Y., Clobert, J., & Julliard, R. (2010). Specialist response to
529 proportion of arable land and pesticide input in agricultural landscapes. *Biological Conservation*, 143,
530 883–890. doi: 10.1016/j.biocon.2009.12.035

531

532 Finnish Environment Institute (2014). CORINE Land Cover 2012 database. Publication date:
 533 11.11.2014. Land cover classification:
 534 http://geoportal.ymparisto.fi/meta/julkinen/dokumentit/CorineLandCover2012_en.pdf
 535
 536 Gabriel, D., & Tscharntke, T. (2007) Insect pollinated plants benefit from organic farming.
 537 Agriculture, Ecosystems and Environment, 118, 43–48. doi: 10.1016/j.agee.2006.04.005
 538
 539 Gagic, V., Kleijn, D., Baldi, A., Boros, G., Bracht Jørgensen, H., Elek, Z., ... Bommarco, R. (2017).
 540 Combined effects of agrochemicals and ecosystem services on crop yield across Europe. Ecology
 541 Letters, 20, 1427–1436. doi: 10.1111/ele.12850
 542
 543 Garibaldi, L., Aizen, M. A., Klein, A. M., Cunningham, S. A., & Harder, L. D. (2011). Global growth and
 544 stability of agricultural yield decrease with pollinator dependence. Proceedings of the National
 545 Academy of Sciences of the United States of America, 108, 5909–5914. doi:
 546 10.1073/pnas.1012431108
 547
 548 Garibaldi, L., Steffan-Dewenter, I., Kremen, C., Morales, J., Bommarco, R., Cunningham, S., ... Klein, A.
 549 M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey
 550 bee visits. Ecology Letters, 14, 1062–1072. doi: 10.1111/j.1461-0248.2011.01669.x
 551
 552 Genung, M. A., Fox, J., Williams, N. M., Kremen, C., Ascher, J., Gibbs, J., & Winfree, R. (2017). The
 553 relative importance of pollinator abundance and species richness for the temporal variance of
 554 pollination services. Ecology, 98, 1807–1816. doi: 10.1002/ecy.1876
 555
 556 Godfray, H. C. J., Blacquière, T., Field, L. M., Hails, R. S., Potts, S. G., Raine, N.E., ... McLean, A.R.
 557 (2015). A restatement of recent advances in the natural science evidence base concerning

neonicotinoid insecticides and insect pollinators. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151821. doi: 10.1098/rspb.2015.1821

Goulson, D. (2015). Neonicotinoids impact bumblebee colony fitness in the field; a reanalysis of the UK's Food & Environment Research Agency 2012 experiment. *PeerJ*, 3, e854. doi: 10.7717/peerj.854

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, 347, 1255957. doi: 10.1126/science.1255957

Heinrich, B. (1979). "Majoring" and "Minoring" by Foraging Bumblebees, *Bombus Vagans*: An Experimental Analysis. *Ecology*, 60, 245–255. doi: 10.2307/1937652

Hokkanen, H. M. T., Menzler-Hokkanen, I., & Keva, M. (2017). Long-term yield trends of insect-pollinated crops vary regionally and are linked to neonicotinoid use, landscape complexity, and availability of pollinators. *Arthropod-Plant Interactions*, 11, 449–461. doi: 10.1007/s11829-017-9527-3

IPBES (2016). The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. S. G. Potts, V. L. Imperatriz-Fonseca, & H. T. Ngo (Eds). Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Kaukoranta, T., & Hakala, K. (2008). Impact of spring warming on sowing times of cereal, potato and sugar beet in Finland. *Agricultural and Food Science*, 17, 165–176. doi: 10.2137/145960608785328198

584 Ketola, J., Hakala, K., Ruottinen, L., Ojanen, H., Rämö, S., Jauhiainen, L., ... Pelkonen, S. (2015). The
 585 impact of the use of neonicotinoid insecticides on honey bees in the cultivation of spring oilseed
 586 crops in Finland in 2013–2015. *Natural resources and bioeconomy studies*, 73/2015. Helsinki,
 587 Finland: Natural Resources Institute Finland (Luke).
 588
 589 Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., &
 590 Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings*
 591 *of the Royal Society B: Biological Sciences*, 274, 303–313. doi: 10.1098/rspb.2006.3721
 592
 593 Knodel, J. J., Olson, D. L., Hanson, B. K., & Henson, R. A. (2008). Impact of planting dates and
 594 insecticide strategies for managing crucifer flea beetles (Coleoptera: Chrysomelidae) in spring-
 595 planted canola. *Journal of Economic Entomology*, 101, 810–821. doi: 10.1093/jee/101.3.810
 596
 597 Kőrösi, Á., Markó, V., Kovács-Hostyánszki, A., Somay, L., Varga, Á., Elek, Z., Boreux, V., Klein, A.,
 598 Földesi, R., Báldi, A. (2018). Climate-induced phenological shift of apple trees has diverse effects on
 599 pollinators, herbivores and natural enemies. *PeerJ*, 6, e5269. doi: 10.7717/peerj.5269
 600
 601 Korpela, S. (1988). The influence of honeybee pollination on turnip rape (*Brassica campestris*) yield
 602 and yield components. *Annales Agriculturae Fenniae*, 27, 295–303.
 603
 604 Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A., Settele, J., Kremen, C., & Dicks, L. V. (2017).
 605 Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and
 606 pollination. *Ecology Letters*, 20, 673–689. doi: 10.1016/j.tree.2012.10.012
 607
 608 Natural Resources Institute Finland (2018). Utilised Agricultural Area 2017.
 609 http://stat.luke.fi/en/utilised-agricultural-area-2017_en Last accessed: 15.1.2019

610

611 Lechenet, M., Dessaint, F., Py, G., Makowski, D., & Munier-Jolain, N. (2017). Reducing pesticide use
612 while preserving crop productivity and profitability on arable farms. *Nature Plants*, 3, 17008. doi:
613 10.1038/nplants.2017.8

614

615 Lundin, O., Myrbeck, Å., & Bommarco, R. (2018). The effects of reduced tillage and earlier seeding on
616 flea beetle (*Phyllotreta* spp.) crop damage in spring oilseed rape (*Brassica napus* L.). *Crop Protection*,
617 107, 104–107. doi: 10.1016/j.cropro.2017.10.019

618

619 Marini, L., Tamburini, G., Petrucco-Toffolo, E., Lindström, S. A., Zanetti, F., Mosca, G., ... Bommarco,
620 R. (2015). Crop management modifies the benefits of insect pollination in oilseed rape. *Agriculture*,
621 *Ecosystems and Environment*, 207, 61–66. doi: 10.1016/j.agee.2015.03.027

622

623 McGregor, D. I. (1981). Pattern of flower and pod development in rapeseed. *Canadian Journal of*
624 *Plant Science*, 61, 275–282. doi: 10.4141/cjps81-040

625

626 Memmott, J., Craze, P.G., Waser, N.M., & Price, M.V. (2007) Global warming and the disruption of
627 plant-pollinator interactions. *Ecology Letters*, 10, 710–717. doi: 10.1111/j.1461-0248.2007.01061.x

628

629 Nicholson, C. C., Koh, I., Richardson, L. L., Beauchemin, A., & Ricketts, T. H. (2017). Farm and
630 landscape factors interact to affect the supply of pollination services. *Agriculture, Ecosystems and*
631 *Environment*, 250, 113–122. doi: 10.1016/j.agee.2017.08.030

632

633 Öckinger, E., Lindborg, R., Sjödin, N. E., Bommarco, R. (2012). Landscape matrix modifies richness of
634 plants and insects in grassland fragments. *Ecography*, 35, 259–267. doi: 10.1111/j.1600-
635 0587.2011.06870.x

636

637 Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E., & Danforth, B. N. (2015). Negative effects of pesticides
638 on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B:*
639 *Biological Sciences*, 282, 20150299. doi: 10.1098/rspb.2015.0299

640

641 Petanidou, T., Kallimanis, A. S., Sgardelis, S. P., Mazaris, A. D., Pantis, J. D., & Waser, N. M. (2014).
642 Variable flowering phenology and pollinator use in a community suggest future phenological
643 mismatch, *Acta Oecologica*, 59, 104–111. doi: 10.1016/j.actao.2014.06.001

644

645 Pettis, J. S., Lichtenberg, E. M., Andree, M., Stitzinger, J., Rose, R., & Vanengelsdorp, D. (2013). Crop
646 pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen
647 *Nosema ceranae*. *PLOS ONE*, 8, e70182. doi: 10.1371/journal.pone.0070182

648

649 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2017). *_nlme: Linear and Nonlinear*
650 *Mixed Effects Models_*. R package version 3.1–131.

651

652 Pisa, L. W., Amaral-Rogers, V., Belzunces, L. P., Bonmatin, J. M., Downs, C. A., Goulson, D., ...
653 Wiemers, M. (2015). Effects of neonicotinoids and fipronil on non-target invertebrates.
654 *Environmental Science and Pollution Research*, 22, 68–102. doi: 10.1007/s11356-014-3471-x

655

656 Pisanty, G., Afik, O., Wajnberg, E., Mandelik, Y., & Diekötter, T. (2015). Watermelon pollinators
657 exhibit complementarity in both visitation rate and single-visit pollination efficiency. *Journal of*
658 *Applied Ecology*, 53, 360–370. doi: 10.1111/1365-2664.12574

659

660 Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., ...
 661 Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540,
 662 220–229. doi: 10.1038/nature20588
 663
 664 Raimets, R., Karise, R., Mänd, M., Kaart, T., Ponting, S., Song, J., & Cresswell, J. E. (2018). Synergistic
 665 interactions between a variety of insecticides and an ergosterol biosynthesis inhibitor fungicide in
 666 dietary exposures of bumble bees (*Bombus terrestris* L.). *Pest Management Science*, 74, 541–546.
 667 doi: 10.1002/ps.4756
 668
 669 R Core Team (2017). R: A language and environment for statistical computing. R Foundation for
 670 Statistical Computing. Vienna, Austria.
 671
 672 Redhead, J. W., Dreier, S., Bourke, A. F. G., Heard, M. S., Jordan, W. C., Sumner, S., ... Carvell, C.
 673 (2016). Effects of habitat composition and landscape structure on worker foraging distances of five
 674 bumble bee species. *Ecological Applications*, 26, 726–739. doi: 10.1890/15-0546
 675
 676 Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., ...
 677 Viana, B. F. (2008). Landscape effects on crop pollination services: are there general patterns?
 678 *Ecology Letters*, 11, 499–515. doi: 10.1111/j.1461-0248.2008.01157.x
 679
 680 Rundlöf, M., Andersson, G. K., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., ... Smith, H. G.
 681 (2015). Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature*, 521, 77–
 682 80. doi: 10.1038/nature14420
 683

684 Stanley, D. A., Garratt, M. P. D., Wickens, J. B., Wickens, V. J., Potts, S. G., & Raine, N. E. (2015).
 685 Neonicotinoid pesticide exposure impairs crop pollination services provided by bumblebees. *Nature*,
 686 528, 548–550. doi: 10.1038/nature16167
 687
 688 Svensson, B., Lagerlof, J., & Svensson, B. G. (2000). Habitat preferences of nest-seeking bumble bees
 689 (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems and Environment*, 77,
 690 247–255. doi: 10.1016/S0167-8809(99)00106-1
 691
 692 Tittone, P. (2014). Ecological intensification of agriculture — sustainable by nature. *Current Opinion*
 693 *in Environmental Sustainability*, 8, 53–61. doi: 10.1016/j.cosust.2014.08.006
 694
 695 Toivonen, M., Herzog, I., Rajanen, H., Toikkanen, J., & Kuussaari, M. (2019). Turnip rape pollination
 696 data, Finland 2017. Knowledge Network for Biocomplexity. doi: 10.5063/F1445JRF
 697
 698 Toivonen, M., Peltonen, A., Herzog, I., Heliölä, J., Leikola, N., Kuussaari, M. (2017). High cover of
 699 forest increases the abundance of most grassland butterflies in boreal farmland. *Insect Conservation*
 700 *and Diversity*, 10, 321–330. doi: 10.1111/icad.12226
 701
 702 Tosi, S., Costa, C., Vesco, U., Quaglia, G., & Guido, G. (2018). A 3-year survey of Italian honey bee-
 703 collected pollen reveals widespread contamination by agricultural pesticides. *Science of the Total*
 704 *Environment*, 615, 208–218. doi: 10.1016/j.scitotenv.2017.09.226
 705
 706 Tukes (2016). Tukesilta poikkeuslupa öljykasvien peittausaineille. Ammattilaistiedote 30.11.2016.
 707 [Tukes grants a temporary authorization for seed treatment products of oilseed crops. Information
 708 release 30.11.2016]. The Finnish Safety and Chemicals Agency (Tukes). [https://tukes.fi/artikkeli/-](https://tukes.fi/artikkeli/-/asset_publisher/tukesilta-poikkeuslupa-oljykasvien-peittausaineil-1)
 709 [/asset_publisher/tukesilta-poikkeuslupa-oljykasvien-peittausaineil-1](https://tukes.fi/artikkeli/-/asset_publisher/tukesilta-poikkeuslupa-oljykasvien-peittausaineil-1) Last accessed: 15.1.2019

710

711 Varis, A.-L. (1995). Abundance, species composition and daily pattern of bees visiting field bean,
712 goat's rue and turnip rape in southern Finland. *Agricultural Science in Finland*, 4, 473–478.

713

714 Westphal, C. , Steffan-Dewenter, I., & Tscharntke, T. (2009). Mass flowering oilseed rape improves
715 early colony growth but not sexual reproduction of bumblebees. *Journal of Applied Ecology*, 46,
716 187–193. doi: 10.1111/j.1365-2664.2008.01580.x

717

718 Williams, I. H. (1978). The pollination requirements of swede rape (*Brassica napus* L.) and of turnip
719 rape (*Brassica campestris* L). *The Journal of Agricultural Science*, 91, 343–348. doi:
720 10.1017/S0021859600046438

721

722 Williams, I. H., & Free, J. B. (1979). Compensation of oil-seed rape (*Brassica napus*
723 L.) plants after damage to their buds and pods. *The Journal of Agricultural Science*, 92, 53–59. doi:
724 10.1017/S0021859600060494

725

726 Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2007). Native bees provide insurance against
727 ongoing honey bee losses. *Ecology Letters*, 10, 1105. doi: 10.1111/j.1461-0248.2007.01110.x

728

729 Wood, T. J., & Goulson, D. (2017). The environmental risks of neonicotinoid pesticides: a review of
730 the evidence post 2013. *Environmental Science and Pollution Research International*, 24, 17285–
731 17325. doi: 10.1007/s11356-017-9240-x

732

733 Woodcock, B. A., Bullock, J. M., Shore, R. F., Heard, M. S., Pereira, M. G., Redhead, J., ... Pywell, R. F.
734 (2017). Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science*,
735 30, 1393–1395. doi: 10.1126/science.aaa1190

736

737 Zou, Y., Xiao, H., Bianchi, F. J. J. A., Jauker, F., Luo, S., & van der Werf, W. (2017). Wild pollinators

738 enhance oilseed rape yield in small-holder farming systems in China. *BMC Ecology*, 17, 6. doi:

739 10.1186/s12898-017-0116-1

740