

Review

Benefits of Insect Pollination in Brassicaceae: A Meta-Analysis of Self-Compatible and Self-Incompatible Crop Species

Francisco Rubén Badenes-Pérez 

Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, 28006 Madrid, Spain; fr.badenes@csic.es

Abstract: This paper reviewed the effects of insect pollination on the yield parameters of plants from the family Brassicaceae presenting different breeding systems. Meta-analysis indicates that in both self-compatible and self-incompatible crop species, meta-analysis indicates that seed yield (Y), silique set (SQS), number of siliquae/plant (NSQ), and the number of seeds/silique (NSSQ) increase when plants are insect-pollinated compared to when there is no insect pollination. The weight of seeds (WS), however, increased in self-incompatible species but not in self-compatible ones as a result of insect pollination. Overall, the percentage of studies showing a positive effect of insect pollination on yield parameters was higher in self-incompatible than in self-compatible species. It was shown that the ability of self-compatible species to reproduce does not fully compensate for the loss of yield benefits in the absence of insect pollination. Cultivated Brassicaceae attract a wide variety of pollinators, with honeybees (*Apis* spp.) such as *A. mellifera* L., *A. cerana* F., *A. dorsata* F., and *A. florea* F. (Hymenoptera: Apidae); other Apidae, such as bumblebees (*Bombus* spp.) (Hymenoptera: Apidae); mining bees (Hymenoptera: Andrenidae); sweat bees (Hymenoptera: Halictidae); and hoverflies (Diptera: Syrphidae) constituting the most common ones. The benefits of insect pollination imply that pollinator conservation programs play a key role in maximizing yield in cruciferous crops.

Keywords: *Brassica* spp.; breeding system; insect pollination; pollinators; yield



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1. Introduction

Pollinators are essential in food production and plant biodiversity conservation [1–3]. More than 78% of angiosperm species are pollinator-dependent [4]. This obligatory and facultative cross-pollination makes insect pollination essential, or at least a positive factor, in maximizing fertilization. Brassicaceae, as most angiosperms, are xenogamous and either require cross-pollination or can be facultatively cross-pollinated [5–8]. With a few exceptions, flowers in the family Brassicaceae have four sepals, four petals diagonally disposed as a cruciform corolla, two carpels, and six stamens arranged in a tetradynamous pattern (four longer inner ones and two shorter outer ones) [9–11]. Except for one species in the genus *Lepidium* [12], plants in the family Brassicaceae have hermaphrodite flowers [13].

Plants in the family Brassicaceae attract a broad diversity of pollinators, including honeybees such as *Apis mellifera* L. (Hymenoptera: Apidae), solitary bees, such as *Andrena* spp. (Hymenoptera: Andrenidae), and hoverflies, such as *Eristalis tenax* L. (Diptera: Syrphidae) [8,14,15]. The family Brassicaceae includes many economically important species, some of which are widely used as vegetables, oils, condiments, or ornamental plants [16,17]. For example, oilseed rape *Brassica napus* L. subsp. *napus*, which is one of the most cultivated oilseed Brassicaceae, has seen the price of its seeds rise by more than 30% in the last three years [18]. To increase crop yield and gross margins in *B. napus*, bee pollination can be more beneficial than pesticide applications [19]. In Ireland, the benefit of insect pollination to *B. napus* yield has been estimated at EUR 3.9 million per year [20]. In Brazil, the benefit of honeybees to *B. napus* yield is above USD 8 million [21]. The potential benefit of pollination is most important in cruciferous crops in which the harvest consists of seeds and fruits

(i.e., siliquae). Among these are all oilseed Brassicaceae, the most important of which is rapeseed, also known as canola, *B. napus* [22]. Other cruciferous oilseed crops include field mustard *Brassica rapa* L. subsp. *oleifera*, synonymous with *Brassica campestris*; Indian mustard *Brassica juncea* (L.) Czern.; Ethiopian mustard *Brassica carinata* A. Braun; camelina *Camelina sativa* L. (Crantz); radish *Raphanus sativus* (L.) Domin; and white mustard *Sinapis alba* L. These oilseed crops can be used for oil, biofuel, and/or lubricant production [23–30]. The seeds of *S. alba* are used for mustard elaboration, and the siliquae of *R. sativus* can be used as a vegetable (Table 1). Yield parameters in the family Brassicaceae are often measured by seed yield, but other yield parameters such as the number of siliquae/plant and seed oil content are also used [31–33].

A recent meta-analysis conducted with *B. napus*, a self-compatible species, showed that pollinator abundance is consistently important in predicting yield in this crop [34]. To date, no meta-analyses have been conducted to examine the effect of insect pollination in yield parameters across the broad spectrum of cruciferous crops, nor have there been meta-analyses examining the effects of insect pollination on yield parameters separately for self-compatible and self-incompatible species. Self-incompatible Brassicaceae species typically have larger flowers than self-compatible ones in order to attract pollinators, with a significantly reduced seed set in the absence of pollinating agents [35,36]. Given the evolutionary advantage of selfing as a reproductive assurance when there is a paucity of pollinators [37], insect pollination is likely to have more marked positive effects on yield parameters in self-incompatible Brassicaceae species than in self-compatible ones.

The purpose of this paper was to synthesize all the available literature regarding the effects of insect pollination on the main yield parameters of crops of the family Brassicaceae and to identify the main taxon groups of pollinators attracted to these crops. Furthermore, a meta-analysis was conducted in order to compare the effects of insect pollination on yield parameters in self-compatible and self-incompatible cruciferous crops. It was hypothesized that the effect of insect pollination on yield parameters will be more significant in self-incompatible species than in self-compatible ones.

2. Methods

The references included in this review were sourced from the Web of ScienceTM and Scopus databases. Additional publications on the topic were found in the social networking site for scientists and researchers ResearchGate. The species found were 10, including *Brassica oleracea* L., *B. carinata*, *B. juncea*, *B. napus*, *B. rapa*, *C. sativa*, *Eruca sativa* Mill., *R. sativus*, *S. alba*, and *Thlaspi arvense* L. (Brassicaceae). *Thlaspi arvense* was, however, not included in the analysis because the only study available [38] did not include all the necessary statistical data for its inclusion. References were not limited by year of publication, with the exception of *B. napus*. In this crop, given the large amount of studies conducted, only studies published from the year 2000 onwards were included in the analysis. As an exception, one publication from 1986 [31] was used for *B. napus* because it also included studies on several crop species included in this review. The studies included in the meta-analysis were published between the years 1986 and 2019 and had been conducted in Brazil, Chile, Finland, Germany, India, Nepal, Pakistan, Serbia, and the UK. Studies on insect pollination and yield parameters from other countries were either unavailable or did not include the necessary statistical data. The latest retrieval date of the reviewed papers was January 2021. The corresponding authors of the 78 publications assessed for eligibility (Figure 1) were in some cases contacted by e-mail to ask for clarifications regarding the type of cultivars used and the statistical analysis presented. The yield parameters examined were: seed yield measured as seed weight (per plant, area, or open flower) (Y); unitary/group weight of seeds (WS, 1, 100, or 1000 seeds) (henceforth when mentioning seed weight alone, the reference will be to this unitary/group measurement of seed weight); number of seeds (per area, plant, or branch) (NSP); number of seeds (per either silique or open flower) (NSSQ); number of siliquae (per either plant or area) (NSQ); silique set (SQS); silique length (SQL); seed germination (G); and oil content (O).

When one publication included research conducted with several cultivars, the study was considered as one, unless the cultivars had for some reason been studied separately (see publications listed in Table 2). Although there can be varying degrees of self-compatibility and self-incompatibility among the species and varieties of Brassicaceae, *B. napus*, *B. juncea*, *B. carinata*, *C. sativa*, and *S. alba* are considered mostly self-compatible [35,38–41], while *B. oleracea*, *B. rapa*, *E. sativa*, and *R. sativus* are considered mostly self-incompatible and thus require cross-pollination [31,35,41]. To identify the main taxon groups of pollinators attracted to crops of the family Brassicaceae, for each study found on the topic, the insect families named among the five top most abundant pollinators were selected for each crop species and country.

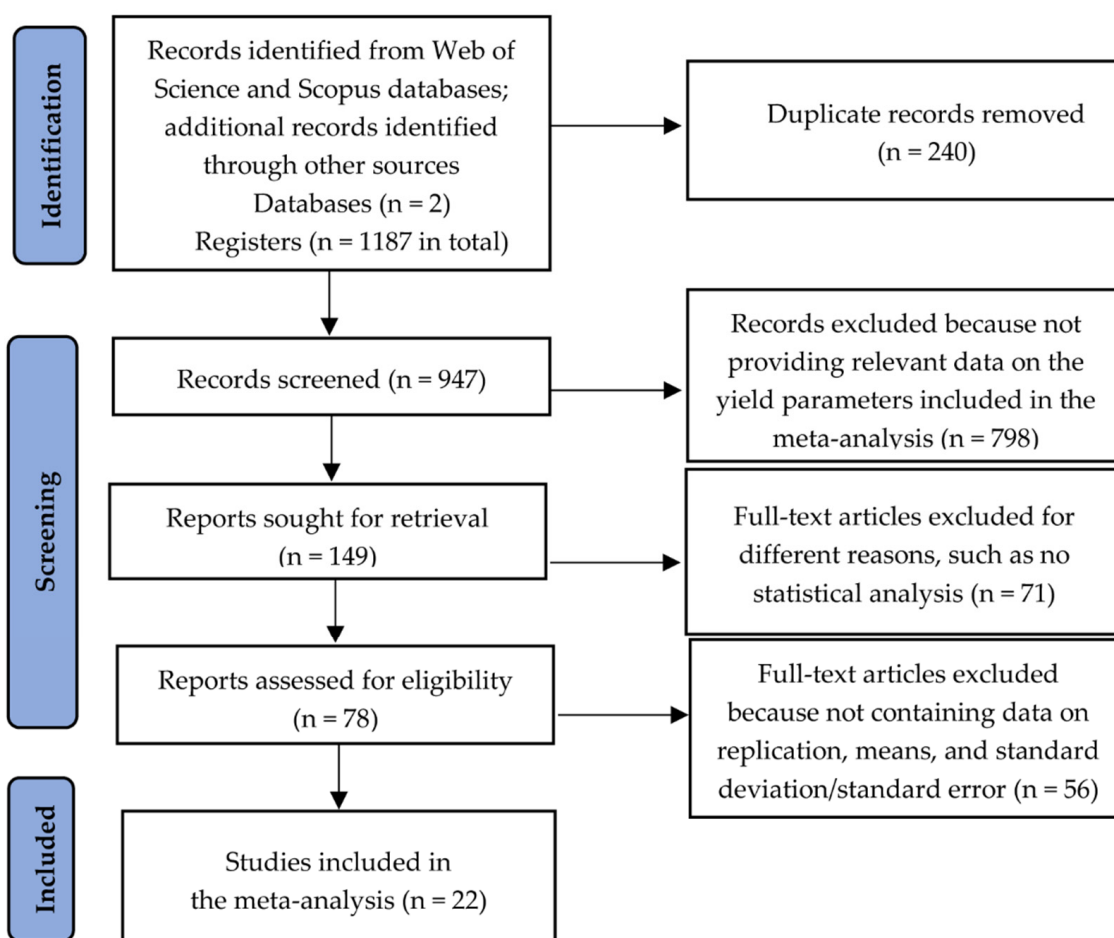


Figure 1. PRISMA flow diagram.

Meta-Analysis

A meta-analysis study was conducted with the main yield parameters reported in the literature separately for self-compatible and self-incompatible species. Since the family Brassicaceae includes both self-compatible and self-incompatible species [35], this allows the possibility of conducting separate meta-analyses for these two groups of crops. As some publications reported, several experiments comparing caged plants without insect pollination versus more than one insect pollination treatment, which were treated as separate studies. Therefore, some publications appeared in a meta-analysis more than once. For this reason, separate entries in the meta-analysis are not necessarily independent. In one of the publications included in the meta-analysis [42], which reported yield data for the lower, middle, and top part of the plant, the data used in the meta-analysis were only those from the middle part of the plant. A random effects model was fitted to the data. All statistical analyses and graphical displays were conducted using Jamovi version 1.6.23 [43].

Forest plots show standardized mean differences (95% confidence intervals, CI), square sizes representing the sample size of each study, and a diamond at the bottom indicating the overall effect size of the meta-analysis. Jamovi uses the R package “metafor”, estimating standardized mean differences by Hedges’ g [44,45]. The amount of heterogeneity was estimated using the restricted maximum-likelihood estimator, providing Cochran’s Q statistic (significant at $p \leq 0.05$) and the I^2 statistic (with values below 25%, between 25% and 50%, and above 75%, considered to indicate low, moderate, and high heterogeneity, respectively) [44,46]. Studies with a Cook’s distance larger than the median plus six times the interquartile range of the Cook’s distances were considered to be overly influential and were removed from the analysis the first time the meta-analysis was run. This happened in the meta-analyses conducted for seed yield in self-compatible and self-incompatible species (two studies removed in each case), the weights of seeds in self-incompatible species (two studies removed), silique set in self-compatible species (two studies removed), and number of seeds/silique in self-incompatible species (one study removed). Funnel plot asymmetry was used to measure differences in effects between smaller and larger studies, for example, because of publication bias [47], and this was assessed by means of the Begg and Mazumdar rank correlation test [48]. A PRISMA flow diagram [49] of the studies included in the meta-analysis is shown below (Figure 1).

Table 1. Most common use and breeding system in the cultivated crops of the family Brassicaceae included in this study. In self-compatible plants, both outcrossing and selfing occurs, while in self-incompatible ones, the main breeding system is outcrossing.

Plant	Most Common Names	Most Common Use	Main Breeding System	References on Breeding System
<i>Brassica carinata</i> A. Braun	Ethiopian mustard	Leaves, seeds for oil	Outcrossing and selfing	[35,40]
<i>Brassica juncea</i> (L.) Czern.	Brown mustard, Indian mustard	Leaves, seeds for oil	Outcrossing and selfing	[35,41]
<i>Brassica napus</i> L.	Rapeseed, canola	Seeds for oil	Outcrossing and selfing	[35,39]
<i>Brassica oleracea</i> L.	Cabbage, broccoli, cauliflower	Leaves, inflorescences	Outcrossing, self-incompatible	[40]
<i>Brassica rapa</i> L.	Turnip, field mustard	Leaves, root, seeds for oil	Outcrossing, self-incompatible	[35,41]
<i>Camelina sativa</i> L. (Crantz)	Camelina, German sesame	Seeds for oil, leaves	Outcrossing and selfing	[35,38]
<i>Eruca sativa</i> Mill.	Arugula, rucola	Leaves	Outcrossing, self-incompatible	[31]
<i>Raphanus sativus</i> (L.) Domin	Radish	Roots, seeds oil	Outcrossing, self-incompatible	[40]
<i>Sinapis alba</i> L.	White mustard	Seeds for table mustard, oil	Outcrossing and selfing	[35,41]

3. Insect Pollination Effect on Yield Parameters in Cultivated Brassicaceae

Table 2 shows the crops for which the effect (increase, decrease, non-significant) of insect pollination on seed yield parameters was studied in the family Brassicaceae (reports from at least seven studies). Of these yield parameters, NSP, SQL, G, and O were subsequently not included in the meta-analysis because, for each of them, there were less than seven publications that reported the statistical parameters necessary to conduct the meta-analysis. Other yield parameters reported in a lesser number of studies (six or fewer studies) included seed weight/plant dry weight, seed weight/silique, number of seeds/plant dry weight, number of siliquae/raceme, silique mass, seed vigor, seed size, percentage of healthy seeds, percentage of filled seeds, oil yield (mg/silique), protein content, flowers/plant, flower abscission, racemes/plant, plant weight and plant dry weight, aboveground biomass, yield/biomass ratio, harvest index (seed weight/aboveground biomass), plant height, and market value (Tables S1–S6).

Table 2. Publications were consulted in this review for the main yield parameters (a total of seven or more studies found) which were: seed yield measured as seed weight/(plant, area, or open flower) (Y); weight of seeds (1, 100, or 1000 seeds) (WS); number of siliquae/(plant or area) (NSQ); number of seeds/(silique or open flower) (NSSQ); silique set (SQS); silique length (SQL); number of seeds/(area, plant, or branch) (NSP); seed germination (G); and oil content of seeds (O). An increase, decrease, or neutral effect of insect pollination on yield parameters is shown in red, blue, or green, respectively. Studies included in the meta-analysis for at least one yield parameter are marked with two asterisks (**) in the Note column.

Plant Species	Yield Parameter							References	Note		
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP			G	O
<i>B. carinata</i>					Red					[31]	**
	Red				Red					[50]	
<i>B. juncea</i>	Red	Red	Red	Red	Red	Green				[31]	**
	Red	Red	Red	Red	Red	Red			Red	[42]	**
		Green	Green		Red			Green		[51]	
		Green			Red					[52]	
			Red	Red	Red					[53]	**
	Red	Red	Red	Red	Red			Red	Red	[54]	**
	Red	Red	Red	Red	Red			Red	Red	[55]	**
	Red	Red	Red	Red	Red			Red	Red	[56]	
	Red	Green						Green	Green	[57]	
	Red	Red		Red	Red				Green	[58]	
			Red	Red					[59]		
<i>B. napus</i>					Red					[31]	**
		Green			Red	Green		Green		[60]	
	Green	Blue		Green	Red		Green			[61]	Male-fertile line
	Red	Blue		Red	Red		Red			[61]	Male-sterile line
	Red	Green	Red	Red	Red		Red			[62]	
		Green	Red	Red	Red		Red			[63]	
	Red	Blue		Red	Red		Red			[64]	
	Red	Blue		Red	Red		Red			[65]	**
				Red	Red		Red			[66]	**
				Red	Red		Red			[67]	**
	Red	Green	Red	Red	Red		Green		Red	[68]	
	Red	Red	Red	Red	Red				Red	[33]	
				Red	Red					[20]	
		Red		Red	Red					[69]	**
	Red	Blue		Red	Red					[70]	**
	Red	Blue		Red	Red					[71]	Hybrid
				Red	Red					[71]	Non-hybrid
				Red	Red					[72]	**
	* Red	* Green			Red					[73]	**
					Green*					[74]	
Red				Red					[75]		
		Red	Red	Red*	Red				[76]	**	
Green			Red	Red				Red	[77]	Hybrid	
Red			Red	Red				Red	[77]	Non-hybrid	
Red	Red		Red	Red			Red	Red	[78]		
Red			Red	Red				Red	[79]		
	Green			Green		Green			[80]		
Green				Green					[81]	Hybrid	
Red			Red	Red					[81]	Non-hybrid	
Red			Red	Red					[82]		
Red	Blue	Red	Green	Red					[83]		
Green	Green		Green	Red			Green		[84]	**	
Green	Green		Green	Red			Green		[85]		
Red	Green	Red		Blue					[86]		
Red			Green	Red					[87]		
	Green		Green	Red				Red	[88]		

Table 2. Cont.

Plant Species	Yield Parameter									References	Note
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP	G	O		
<i>B. oleracea</i>										[89]	
										[90]	
										[31]	**
										[91]	
										[92]	Cabbage ** Cauliflower **
<i>B. rapa</i>										[92]	
										[93]	
										[31]	**
										[94]	**
										[95]	**
										[96]	
										[97]	
										[98]	
										[99]	
										[100]	
<i>C. sativa</i>										[101]	
										[102]	**
										[103]	**
										[104]	
										[38]	**
<i>E. sativa</i>									[31]	**	
<i>R. sativus</i>										[31]	**
										[105]	**
										[106]	
										[107]	**
										[108]	**
										[109]	
<i>S. alba</i>										[110]	
										[31]	
										[111]	

* Most common response when several cultivars, planting dates, or experimental locations were used.

The percentage of publications showing an increase, decrease, and neutral effect of insect pollination on the main yield parameters is shown in Figure 2. In this figure, the O yield parameter is not shown for self-incompatible species because only two publications reported on the effect that insect pollination had on this yield parameter in self-incompatible Brassicaceae crops.

3.1. Effect of Insect Pollination on Yield Parameters in Self-Compatible and Self-Incompatible Species

In terms of insect pollination and crop yield, *B. napus* and *B. rapa* were the most studied crops among the self-compatible and self-incompatible Brassicaceae crops, respectively (Table 2, Tables S4 and S5). The meta-analysis evaluation of the effect of insect pollination on the main yield parameters is shown below.

3.1.1. Effect of Insect Pollination on Y

For self-compatible species, a total of seven studies were included in the analysis (Figure 3A). The observed standardized mean differences ranged from 0.93 to 2.99, with all estimates being positive. The estimated average standardized mean difference was 1.95 (95% CI: 1.40–2.49). The average outcome differed significantly from zero ($z = 7.02$, $p \leq 0.001$). According to the Q-test, there was no significant amount of heterogeneity in the true outcomes (Table 3). A 95% prediction interval for the true outcomes was given by 1.02–2.87. The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S1A).

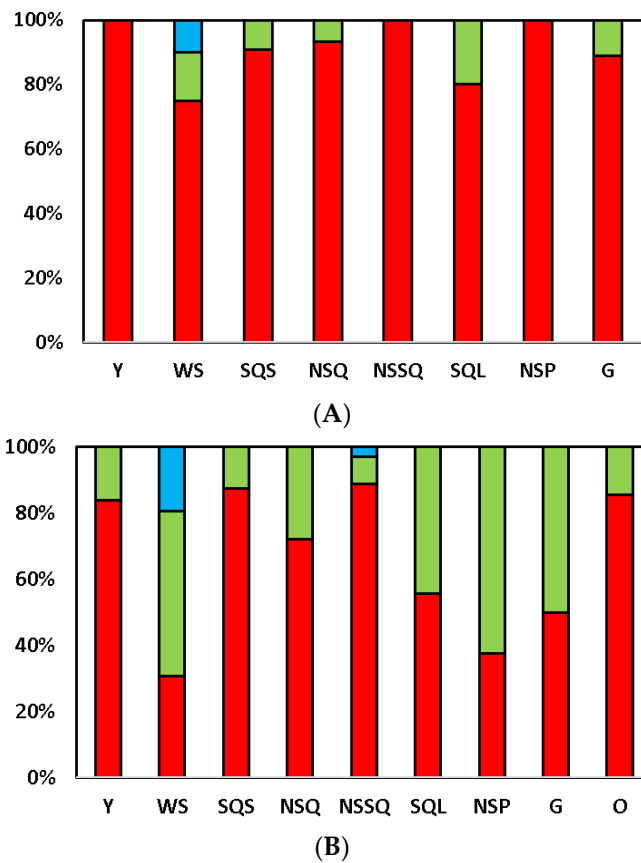


Figure 2. Percentage of publications showing an increased, decreased, and neutral effect of insect pollination on seed yield measured as seed weight/(plant, area, or open flower) (Y); weight of seeds (1, 100, or 1000 seeds) (WS); silique set (SQS); number of siliquae/(plant or area) (NSQ); number of seeds/(silique or open flower) (NSSQ); silique length (SQL); number of seeds/(area, plant, or branch) (NSP); seed germination (G), and oil content (O). An increased, decreased, or neutral effect is shown in red, blue, or green, respectively, in self-compatible (A) and self-incompatible Brassicaceae crops (B).

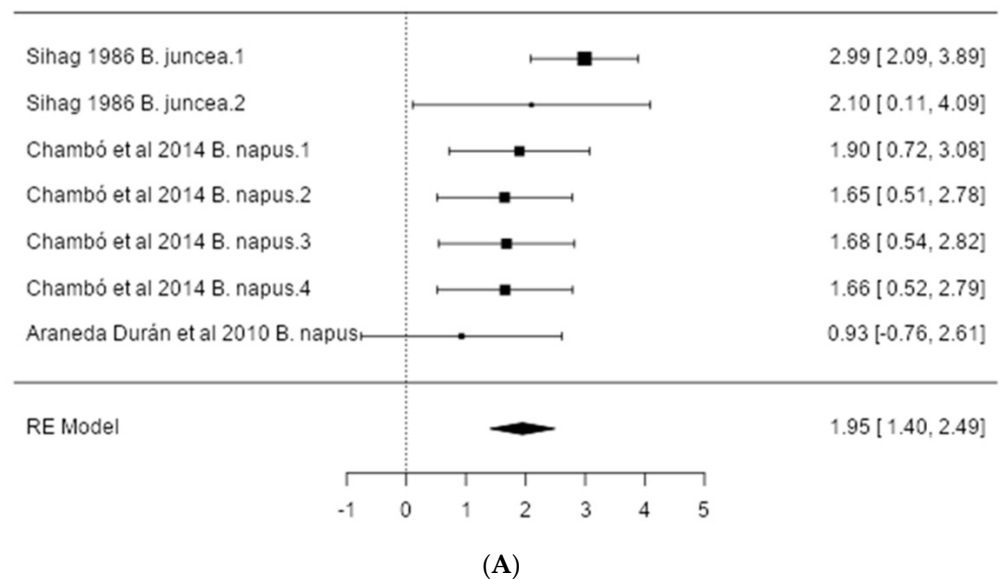


Figure 3. Cont.

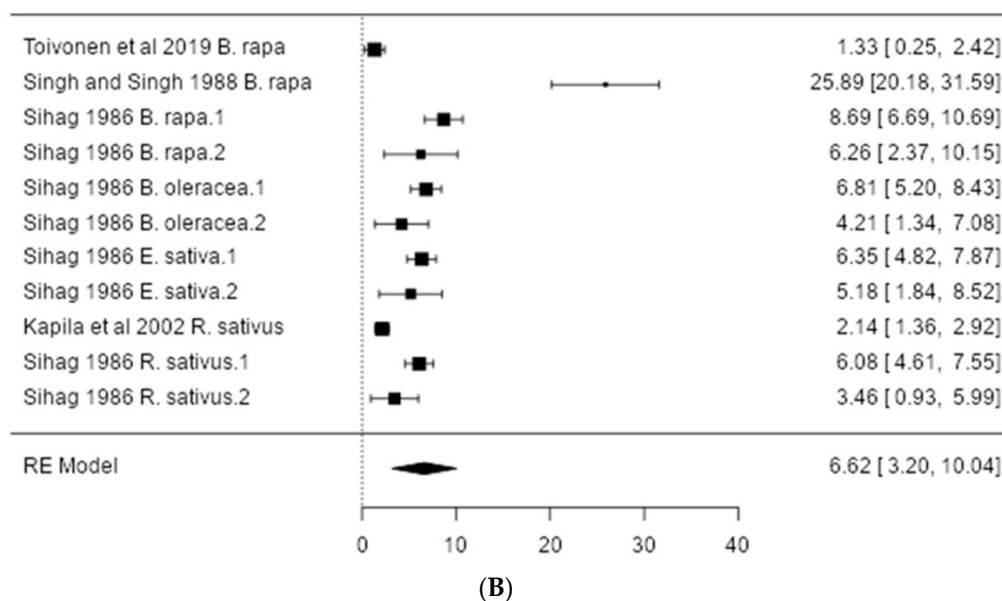


Figure 3. Forest plot of meta-analysis for the effect of insect pollination on seed yield in self-compatible (A) and self-incompatible Brassicaceae crops (B).

Table 3. Heterogeneity statistics and publication bias based on Begg and Mazumdar rank correlation for the meta-analyses conducted to test the effect of insect pollination on yield parameters in self-compatible (SC) and self-incompatible (SI) Brassicaceae. The yield parameters included in the meta-analysis were seed yield measured as seed weight/(plant, area, or open flower) (Y); weight of seeds (WS); silique set (SQS); number of siliquae/(plant or area) (NSQ); and number of seeds/(silique or open flower) (NSSQ).

Yield Parameter and Breeding System	Heterogeneity Statistics						Begg and Mazumdar Rank Correlation	
	Tau ²	SE	df	I ²	Q	p-Value	Value	p-Value
Y SC	0.145	0.302	6	27.36%	7.240	0.299	0.048	1.000
Y SI	31.660	14.988	10	97.75%	153.147	<0.001	0.418	0.087
WS SC	0.661	0.476	10	65.37%	41.585	<0.001	0.091	0.761
WS SI	251.094	122.948	9	99.83%	288.722	<0.001	0.600	0.017
SQS SC	4.586	2.140	11	94.68%	96.480	<0.001	0.424	0.063
SQS SI	9.914	5.783	7	94.98%	127.520	<0.001	0.714	0.014
NSQ SC	6.888	3.319	11	95.21%	251.043	<0.001	0.485	0.031
NSQ SI	111.376	56.969	8	99.59%	1197.316	<0.001	0.500	0.075
NSSQ SC	2.149	0.705	22	98.03%	778.747	<0.001	0.099	0.530
NSSQ SI	7.928	3.193	15	98.53%	294.886	<0.001	0.467	0.011

For self-incompatible species, a total of 11 studies were included in the analysis (Figure 3B). The observed standardized mean differences ranged from 1.33 to 25.89, with all estimates being positive. The estimated average standardized mean difference was 6.62 (95% CI: 3.20–10.04). The average outcome differed significantly from zero ($z = 3.79$, $p \leq 0.001$). According to the Q-test and the high I² statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by −4.93–18.17. The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S1B).

3.1.2. Effect of Insect Pollination on WS

For self-compatible species, a total of 11 studies were included in the analysis (Figure 4A). The observed standardized mean differences ranged from −1.31 to 12.45, with the majority

of estimates being positive (64%). The estimated average standardized mean difference was 0.18 (95% CI: $-0.44-0.80$). The average outcome did not differ significantly from zero ($z = 0.57, p = 0.571$). According to the Q-test and the I^2 , the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes was given by $-1.53-1.89$. The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S2A).

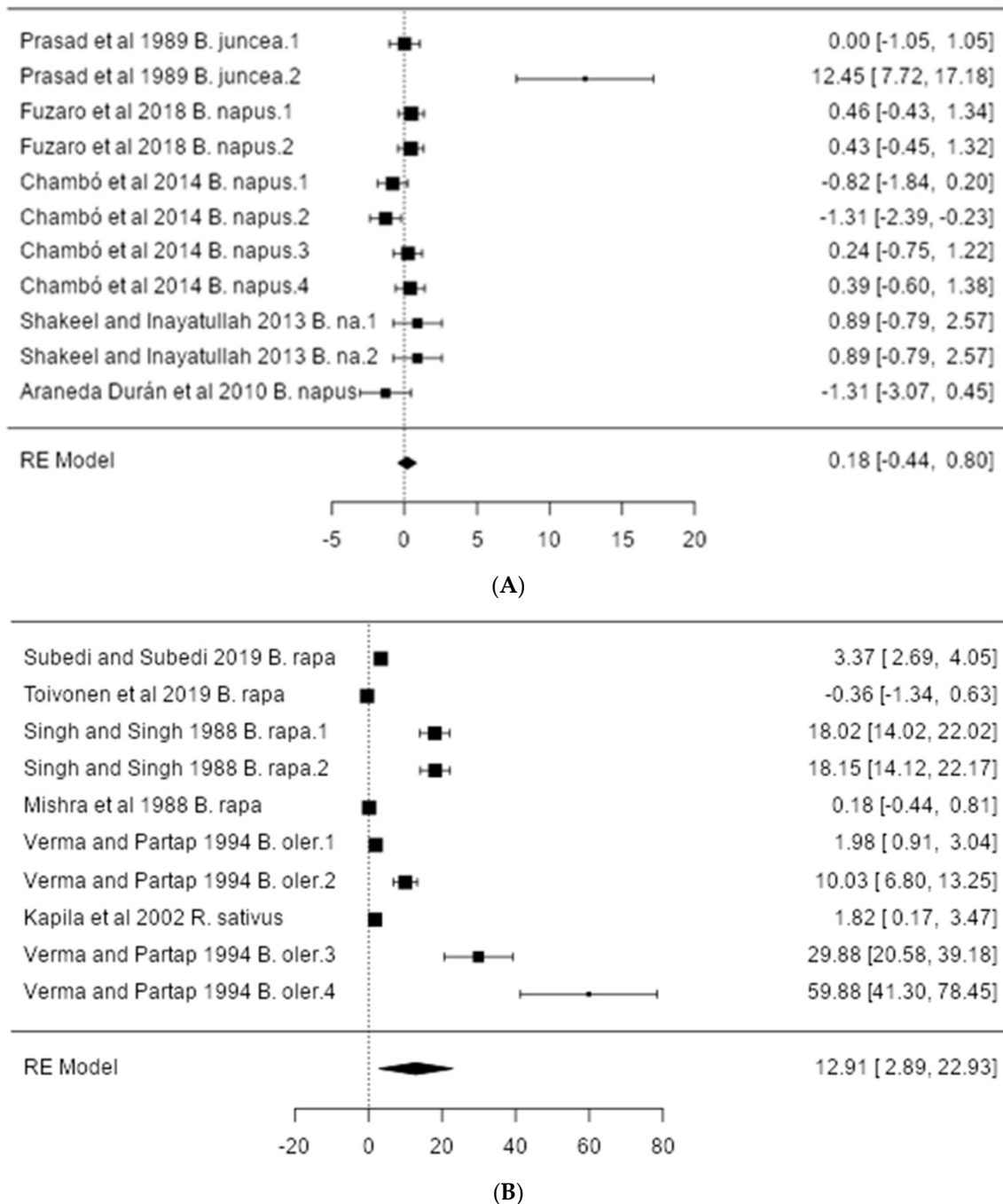


Figure 4. Forest plot of meta-analysis for the effect of insect pollination on the weight of seeds in self-compatible (A) and self-incompatible Brassicaceae crops (B). In some cases *B. napus* and *B. oleracea* have been abbreviated as *B. na.* and *B. oler.*, respectively, to avoid overlapping with error bars and squares.

For self-incompatible species, a total of 10 studies were included in the analysis (Figure 4B). The observed standardized mean differences ranged from -0.36 to 59.87 with the majority of the estimates being positive (90%). The estimated average standardized mean difference was 12.91 (95% CI: 2.89 – 22.93). The average outcome differed significantly from zero ($z = 2.52$, $p = 0.012$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -19.72 – 45.54 . The rank correlation test indicated potential funnel plot asymmetry (Table 3, Figure S2B).

3.1.3. Effect of Insect Pollination on SQS

For self-compatible species, a total of 12 studies were included in the analysis (Figure 5A). The observed standardized mean differences ranged from 0.25 to 8.15 , with all estimates being positive. The estimated average standardized mean difference was 2.19 (95% CI: 0.92 – 3.46). The average outcome differed significantly from zero ($z = 3.38$, $p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -2.19 – 6.58 . The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S3A).

For self-incompatible species, a total of eight studies were included in the analysis (Figure 5B). The observed standardized mean differences ranged from 1.54 – 10.39 , with all estimates being positive. The estimated average standardized mean difference was 5.46 (95% CI: 3.18 – 7.74). The average outcome differed significantly from zero ($z = 4.69$, $p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appeared to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -1.12 – 12.04 . The rank correlation test indicated potential funnel plot asymmetry (Table 3, Figure S3B).

3.1.4. Effect of Insect Pollination on NSQ

For self-compatible species, a total of 12 studies were included in the analysis (Figure 6A). The observed standardized mean differences ranged from 0.71 to 11.94 , with all estimates being positive. The estimated average standardized mean difference was 4.00 (95% CI: 2.41 – 5.58). The average outcome significantly differed from zero ($z = 4.95$, $p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -1.39 – 9.38 . The rank correlation test indicated potential funnel plot asymmetry (Table 3, Figure S4A).

For self-incompatible species, a total of nine studies were included in the analysis (Figure 6B). The observed standardized mean differences ranged from 0.15 to 29.39 , with all estimates being positive. The estimated average standardized mean difference was 14.76 (95% CI: 7.79 – 21.74). The average outcome differed significantly from zero ($z = 4.15$, $p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -7.06 – 36.59 . The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S4B).

3.1.5. Effect of Insect Pollination on NSSQ

For self-compatible species, a total of 23 studies were included in the analysis (Figure 7A). The observed standardized mean differences ranged from -1.23 to 4.20 , with the majority of the estimates being positive (87%). The estimated average standardized mean difference was 1.62 (95% CI: 0.99 – 2.24). The average outcome differed significantly from zero ($z = 5.07$, $p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the true outcomes is given by -1.32 – 4.56 . The rank correlation test indicated that there was no significant funnel plot asymmetry (Table 3, Figure S5A).

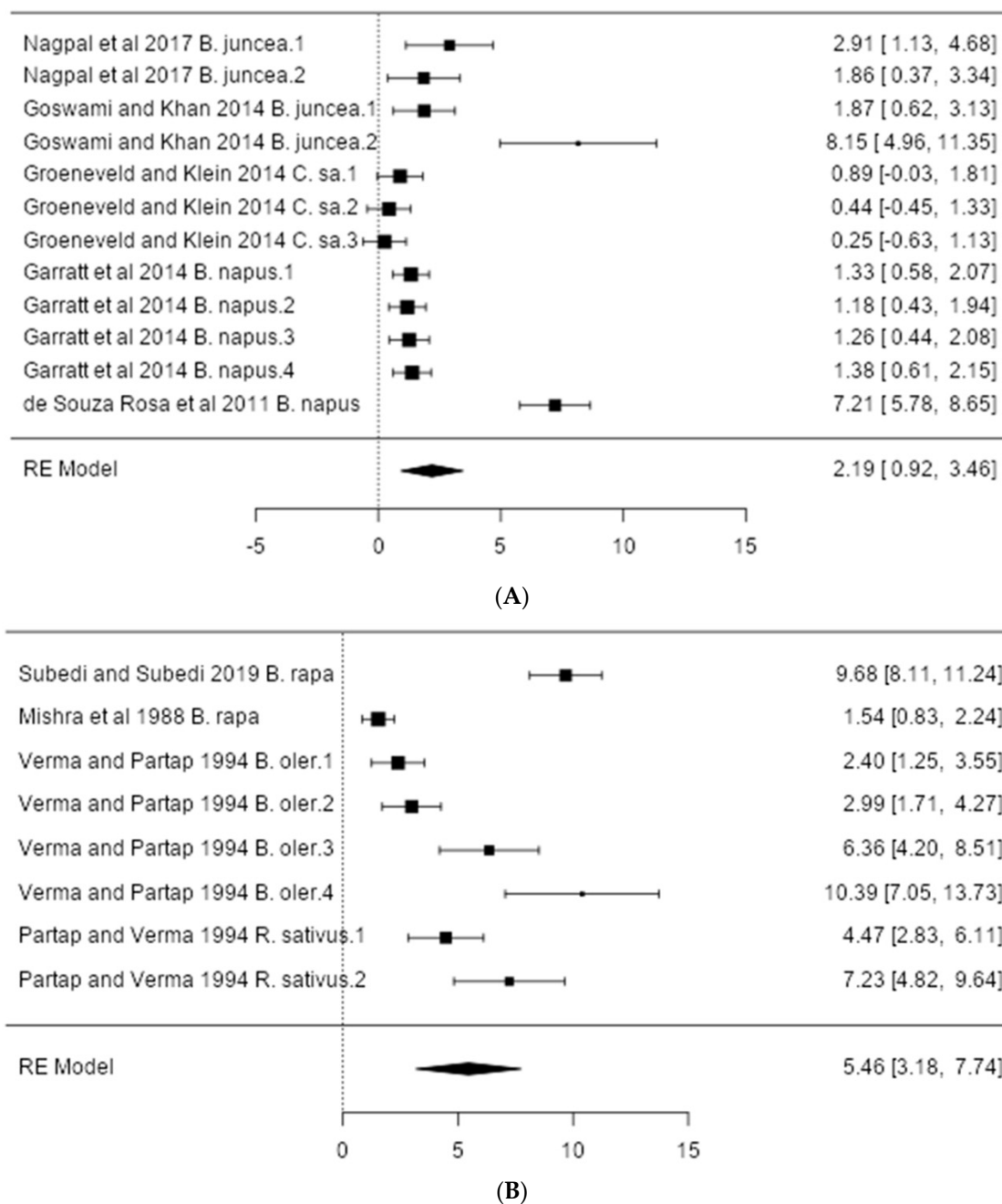


Figure 5. Forest plot of the meta-analysis for the effect of insect pollination on the silique set in self-compatible (A) and self-incompatible Brassicaceae crops (B). In the plots, *B. oleracea* and *C. sativa* are abbreviated to B. oler. and C. sa., respectively, to prevent overlapping with error bars and squares.

For self-incompatible species, a total of 16 studies were included in the analysis (Figure 7B). The observed standardized mean differences ranged from 1.54 to 81.26, with all estimates being positive. The relatively high standardized mean difference value and 95% CI of 81.26 [56.06, 106.46] in the study conducted with cabbage by Verma and Partap [92] was probably due to the large difference in the number of seeds per silique between open-pollinated plants and caged plants not exposed to insect pollination, as there was no silique set and the number of seeds per silique was zero in caged plants. The estimated average standardized mean difference was 5.07 (95% CI: 3.60–6.54). The average outcome differed significantly from zero ($z = 6.75, p \leq 0.001$). According to the Q-test and the high I^2 statistic, the true outcomes appear to be heterogeneous (Table 3). A 95% prediction interval for the

true outcomes is given by -0.65 – 10.78 . The rank correlation test indicated the potential funnel plot asymmetry (Table 3, Figure S5B).

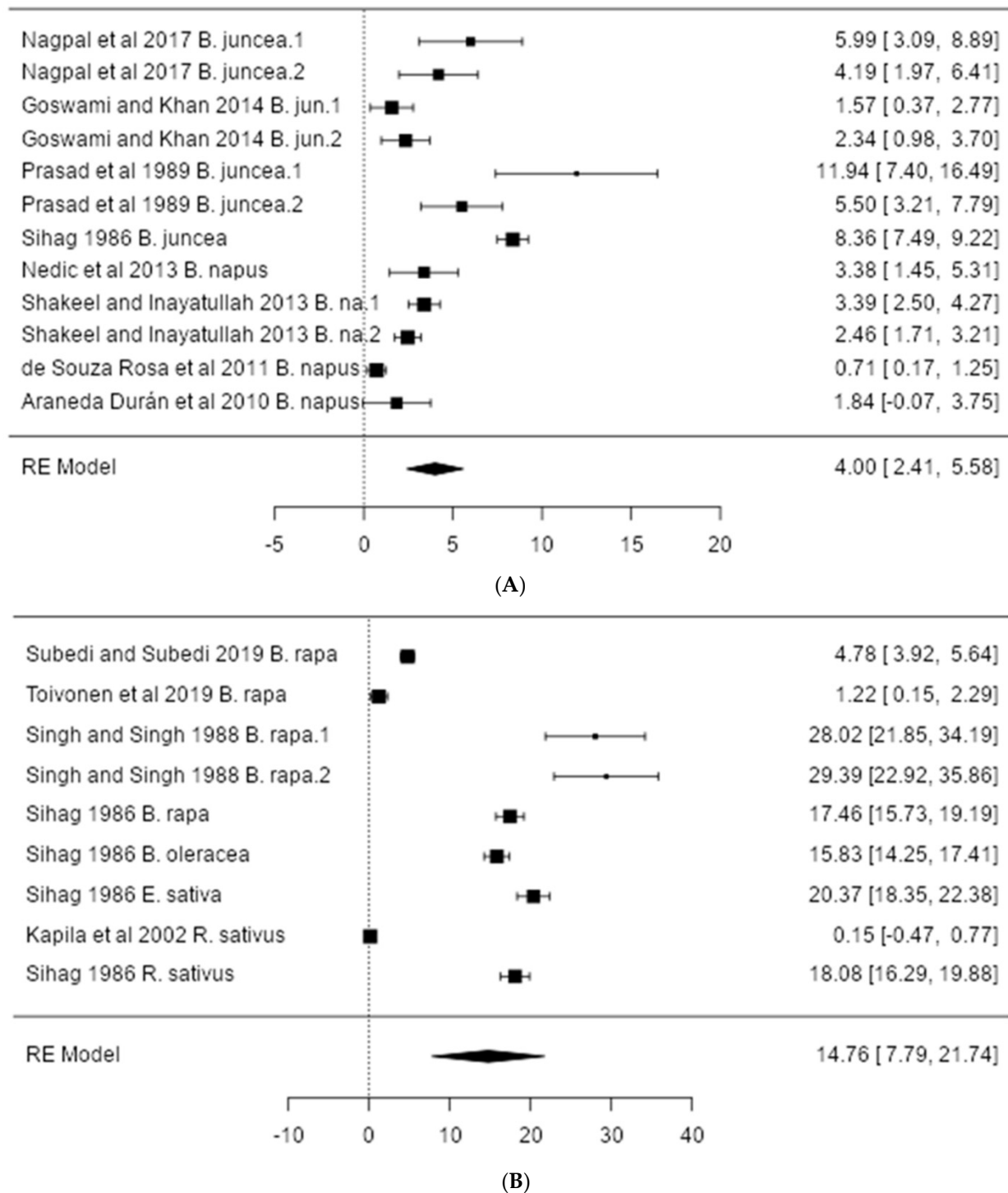


Figure 6. Forest plot of the meta-analysis for the effect of insect pollination on the number of siliquae/plant or area in self-compatible (A) and self-incompatible Brassicaceae crops (B). In some cases, *B. juncea* and *B. napus* were abbreviated to *B. jun.* and *B. na.*, respectively, to avoid overlapping with error bars and squares.

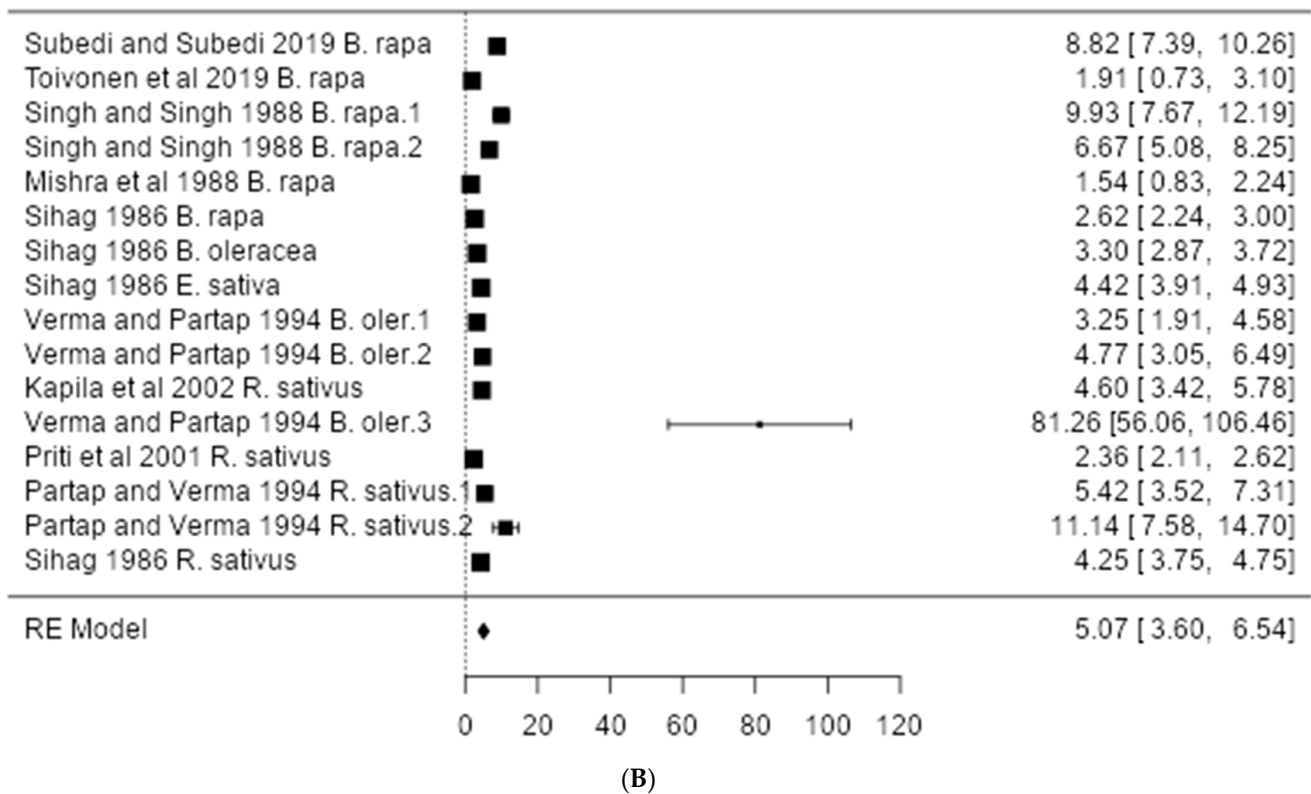
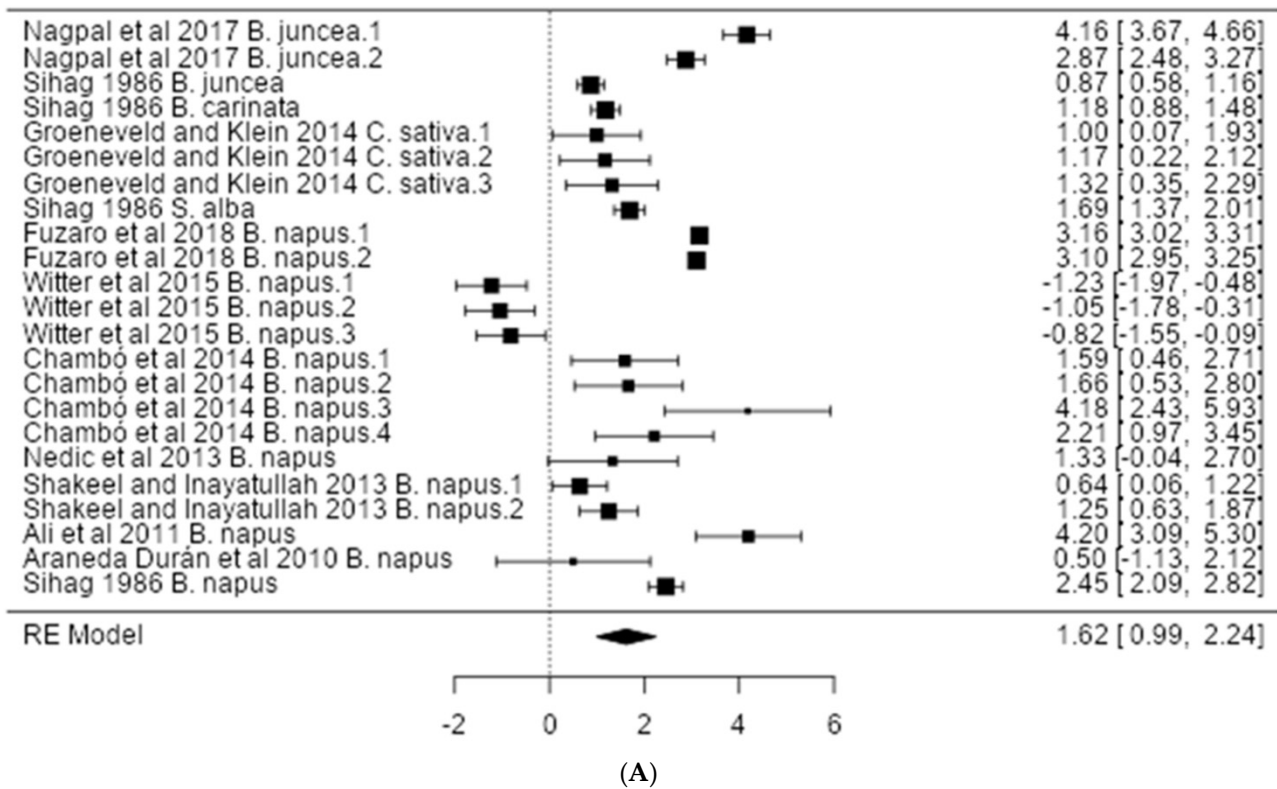


Figure 7. Forest plot of the meta-analysis for the effect of insect pollination on the number of seeds per silique in self-compatible (A) and self-incompatible Brassicaceae crops (B). In some cases, *B. oleracea* has been abbreviated to *B. oler.* to prevent overlapping with error bars and squares.

4. Insect Pollinators of Crops of the Family Brassicaceae

The main pollinators reported for these crops are shown in Table 4, with the top pollinators for all of them being honeybees (*Apis* spp.), such as *A. mellifera*, *A. cerana*., *A. dorsata*, and *A. florea*, and mining bees (Andrenidae). Additional pollinators often reported for these crops are other Apidae (other than *Apis* spp.), such as bumblebees (*Bombus* spp.), sweat bees (Halictidae), and hoverflies (Syrphidae) for *B. juncea*; other Apidae and Syrphidae for *B. napus*; Halictidae and Syrphidae for *B. oleracea*; Syrphidae, Halictidae, and other Apidae for *B. rapa*; Syrphidae and Halictidae for *C. sativa*; other Apidae and Syrphidae for *E. sativa*; and Halictidae and Syrphidae for *R. sativus*. In the case of *B. napus*, single visit pollen deposition has been shown to be the highest for *Bombus* spp., Andrenidae, and *A. mellifera* (with median pollen grain depositions of 341, 335, and 202, respectively) [112], while single visit efficiency in terms of the number of seeds/silique produced was highest for *Halictus* and *Apis* spp. [66]. In *B. napus*, there were no differences in honeybee and bumblebee visits between open-pollinated and hybrid varieties [113], but bee abundance was higher and pollination deficit was lower in conventional compared to genetically modified Roundup Ready plants [114]. In the case of *B. rapa*, efficiency, given by stigmatic pollen grain deposition by a single visit of an insect to a flower, was highest for *Bombus terrestris* L. [15,115]. In addition to efficiency, the abundance and number of insect visits makes some insects more effective pollinators than others. Because of this, *A. mellifera*, often the most common floral visitor, can be considered a more effective pollinator than more efficient pollinators that visit flowers less often [15]. However, one or two bee flower visits may be sufficient to achieve a full seed set in *B. rapa* flowers [116,117].

Table 4. Insect pollinators of crops of the family Brassicaceae. Abbreviations for pollinators are as follows: Apidae of the genus *Apis* (A), other Apidae different than *Apis* spp. (OA), Andrenidae (An), Bibionidae (B), Calliphoridae (C), Coccinellidae (Co), Colletidae (Col), Empididae (E), Formicidae (F), Halictidae (H), Megachillidae (M), Muscidae (Mu), Pieridae (P), Scarabaeidae (S), Sepsidae (Se), Stratiomyidae (St), Syrphidae (Sy), Tabanidae (T), and Vespidae (V). Abbreviations for countries are as follows: Australia (A), Bangladesh (B), Belgium (Be), Brazil (Br), China (C), France (F), Germany (G), India (I), Ireland (Ir), Nepal (N), New Zealand (NZ), Pakistan (P), Sweden (S), United Kingdom (UK), and United States of America (US).

Plant	Number of studies reporting main pollinators in a given family																		Countries	References	
	A	OA	An	B	C	Co	Coll	E	F	H	M	Mu	P	S	Se	St	Sy	T			V
<i>B. carinata</i>	3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I, US	[31,40,50]
<i>B. juncea</i>	14	4	4	-	-	1	-	-	1	3	1	2	-	-	1	-	3	-	1	B, I	[31,40,52,54,56,58,118–126]
<i>B. napus</i>	12	8	4	-	1	-	-	1	-	2	1	1	2	-	-	-	4	-	-	Be, Br, C, F, G, I, Ir, UK, P, S	[20,31,33,40,66,67,127–133]
<i>B. oleracea</i>	8	1	2	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	I	[31,91,93,134–138]
<i>B. rapa</i>	11	5	3	-	-	1	2	-	-	3	1	-	-	2	-	1	7	1	-	A, I, N, NZ, P	[15,31,40,97,103,104,115–117,120,139–142]
<i>C. sativa</i>	2	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	Be, G, US	[38,143–146]
<i>E. sativa</i>	3	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	I, P	[31,40,141]
<i>R. sativus</i>	4	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	I, P	[31,40,107,108]
<i>S. alba</i>	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I	[31,40]
Total	59	19	22	1	1	2	2	1	1	13	3	3	2	2	1	1	20	1	1		

5. Discussion and Main Conclusions

Approximately 75% of crop species benefit from pollinators, contributing to an estimated 9.5% of the value of the world agriculture production devoted to human food [1,147]. Other studies conducting meta-analysis have also shown the benefits of insect pollination for plant reproduction and yield in crops in general [148–150], in the plant species of particular natural habitats [151], and in particular crops, such as fava bean [152], oilseed rape [34], and tomato [153]. This review and meta-analysis shows that, overall, the yield parameters of crops in the family Brassicaceae benefit from insect pollination. Insect pollination has a positive effect on Y, SQS, NSQ, and NSSQ in both self-compatible and self-incompatible cruciferous crops. WS, however, increased as a result of insect pollination only in self-incompatible species. Even though the meta-analysis was conducted with crop species grouped into self-compatible and self-incompatible ones, it indicates that significant yield benefits of insect pollination also occur at the level of individual cruciferous crops.

Plants have evolved to have self-compatibility as a reproductive assurance that gives them a fitness advantage when ovules are outcross-pollen-limited [37]. However, this review shows that in self-compatible species, most yield parameters continue to benefit from insect pollination. Because of this, in some self-compatible crop species such as *B. napus*, the placement of honeybee colonies next to fields has been recommended [62,154]. Regarding the overall neutral effect of insect pollination on WS in self-compatible species, it is known that plants can compensate for variation among some yield parameters [62,63,85]. For example, WS is negatively correlated with NSP and NSSQ in *B. napus* [62,63,85]. This negative correlation indicates that *B. napus* can produce heavier seeds when the seed set is low [62,65,155]. For this reason, even if insect pollination does not increase WS, an increase in NSP can result in a positive effect on Y [62,86]. Another benefit of insect pollination shown for *B. napus* is the shortening of the flowering period and, therefore, of the growing season [87,156,157]. On the other hand, delayed maturity can also increase Y [158].

Except in the case of Y in self-compatible species, a significant amount of heterogeneity (given by the significance of the Q-test and the moderate to high I^2 statistic) was found in the meta-analyses. Furthermore, for NSQ in self-compatible species, and for WS, SQS, and NSSQ in self-incompatible ones, significant asymmetry in the funnel plots (given by the significance of the Begg and Mazumdar rank correlation test) was found. Among the possible reasons explaining this significant heterogeneity and funnel plot asymmetry could be differences in sample size among studies and the high variability of results in yield parameters shown in some studies in the presence and absence of insect pollination. This high variability was more marked in the case of self-incompatible species. This could be an explanation of why funnel plot asymmetry occurred more often in self-incompatible species (occurring for WS, SQS, and NSSQ, i.e., in three out of the six yield parameters examined in the meta-analysis) than in self-compatible ones (occurring only for NSQ, i.e., in one out of six yield parameters examined). Some studies conducted with self-incompatible species and included in the meta-analyses reported SQS values of zero in the absence of insect pollination [92,105]. Low SQS in the absence of insect pollination has been shown for self-incompatible species in other studies [35]. For example, in the absence of insect pollination, the maximum SQS was 17% in self-incompatible species, and in some cases the few siliques produced had either very few or no seeds [35]. On the other hand, in the absence of insect pollination, self-compatible species had at least 43–90% of the silique set [35]. Although this review and meta-analysis only includes crops, given the closeness of the species within the family, the positive effects of insect pollination on yield parameters are also likely to occur in wild Brassicaceae, most of which are considered self-incompatible [159]. The positive effects of insect pollination on seed yield parameters have been found even in self-compatible wild Brassicaceae such as *Lobularia maritima* (L.) Desv. [160,161].

Both honeybees and wild bees are considered important pollinators of crops [148,162–164]. Among the variety of pollinators attracted to flowers of cultivated Brassicaceae, honeybees, *A. mellifera* and other *Apis* spp., seem to be the dominant reported species. However, other Apidae, such as bumblebees, mining bees (Andrenidae), sweat bees (Halictidae),

and hoverflies (Syrphidae) are also commonly reported as pollinators of these crops. Since *A. mellifera* is often the most common floral visitor, the higher frequency of visits can make it a more effective pollinator than other more efficient pollinators that visit flowers less often [15,135–137]. Other pollinator families, such as Lepidoptera, were not among the most abundant pollinators found in the studies reviewed. However, lepidopterans such as *Pieris* spp. (Lepidoptera: Pieridae) were sometimes reported among less common pollinators [58,132,140]. Pollinator diversity can also enhance crop pollination and yield [34].

The importance of pollinators for yield in Brassicaceae crops makes it paramount to ensure that agricultural practices are compatible with pollinator conservation. Pest management and other agricultural practices can affect the effect of pollination on yield, and this has been shown for *B. napus* [75,79,85,165,166] and *B. rapa* [102,114]. In general, the application of pesticides, if unavoidable, should be performed following practices that minimize the risk of pollinator poisoning, such as using pesticides of low toxicity and not spraying when bees are foraging [14,101,167,168]. Unfortunately, some farmers growing cruciferous crops are unaware of the harmful effects that pesticide applications can have on pollinators and other beneficial insects [169,170]. Pollinator conservation practices, such as setting pollinator reservoirs [171–173], could also be implemented in the vicinity of Brassicaceae crops to ensure that pollinators can be sustained throughout the year. Pollinator reservoirs can also help in conservation biological control [174,175]. Some of the crops included in this review, such as *B. rapa* and *S. alba*, have also been used as insectary plants [176]. Proximity to natural habitats with natural vegetation and where wild bees can locate their nests can also enhance the abundance of wild bees [104,115,128]. The flowers of crucifer crops can also temporarily benefit wild bees because of the food resource boost [129].

In conclusion, a meta-analysis shows that insect pollination has a positive effect on Y, SQS, NSQ, and NSSQ in both self-compatible and self-incompatible cruciferous crops. WS increased as a result of insect pollination only in self-incompatible species. Given the reproductive advantage of self-compatibility in the absence of pollinators, insect pollination could have more positive effects on yield parameters in self-incompatible species than in self-compatible ones. However, among the yield parameters investigated, WS was the only one that did not improve in self-compatible species as a result of insect pollination. In Brassicaceae crops, the insect families most reported as pollinators are Apidae, Andrenidae, Syrphidae, and Halictidae.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/agriculture12040446/s1>, Table S1: Studies reporting on insect pollination and yield parameters in *Brassica carinata*, *Camelina sativa*, *Eruca sativa*, and *Sinapis alba*; n/a = information not available; Table S2: Studies reporting on insect pollination and yield parameters in *Brassica juncea*; n/a = information not available; Table S3: Studies reporting on insect pollination and yield parameters in *Brassica napus*. Except for Sihag et al., the references are from the year 2000 onwards; n/a = information not available; Table S4: Studies reporting on insect pollination and yield parameters in *Brassica oleracea*; n/a = information not available; Table S5: Studies reporting on insect pollination and yield parameters in *Brassica rapa* (synonymous of *Brassica campestris*); n/a = information not available; Table S6: Studies reporting on insect pollination and yield parameters in *Raphanus sativus*; n/a = information not available; Figure S1: Funnel plots corresponding to the meta-analyses of the effect of insect pollination on seed yield in self-compatible (A) and self-incompatible (B) Brassicaceae crops; Figure S2: Funnel plots corresponding to the meta-analyses of the effect of insect pollination on the weight of seeds in self-compatible (A) and self-incompatible (B) Brassicaceae crops; Figure S3: Funnel plots corresponding to the meta-analyses of the effect of insect pollination on the silique set in self-compatible (A) and self-incompatible (B) Brassicaceae crops; Figure S4: Funnel plots corresponding to the meta-analyses of the effect of insect pollination on the number of siliques/plant or area in self-compatible (A) and self-incompatible (B) Brassicaceae crops; Figure S5: Funnel plots corresponding to the meta-analyses of the effect of insect pollination on the number of seeds per silique or area in self-compatible (A) and self-incompatible (B) Brassicaceae crops.

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