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Review of methods to investigate pollinator dependency in oilseed rape (*Brassica napus*)

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ABSTRACT

Insects contribute to the pollination of about 75% of crop species. Among such insect-pollinated crops, oilseed rape (*Brassica napus*) is increasingly cultivated worldwide. However, the degree to which seed set in *B. napus* depends on insect pollination is still under debate. To compare research approaches for estimating pollinator dependency, we reviewed the relevant literature published between 1956 and 2018. The majority of the studies were conducted in Europe (75%) on winter cultivars (77%) and monitored honeybees (52%). Our main findings are: (1) Dependency on insect pollination differs among cultivars and regions. (2) Field observations provide more realistic and comparable results than observations on caged plants. (3) Field conditions, soil nutrient availability, and pest management practices all influence insect dependency and subsequent yield. (4) Plot size conditions pollinator behaviour, as pollination success can be related to insect density or diversity depending on the size of the plot. (5) Insect numbers vary according to the observation distances within a field. (6) Comparison between studies is complicated by the use of different proxies to assess final yield, which may not be equivalent. We provide several recommendations to improve the reliability of future studies of oilseed rape pollination and of insect pollination dependency such as choosing open field observations compared to bag, cage or greenhouse studies, registering field conditions (pests, pesticides, fertilisation level) and defining yield as total seeds per plant to take into consideration compensation mechanisms.

1. Introduction

Except the largest wind-pollinated crops belonging to the grass family (cereals, rice, sugar cane, corn), the vast majority of crops are insect-pollinated (Gallai et al., 2009; Garibaldi et al., 2011; Klein et al., 2007; Roubik et al., 2018). Moreover, the proportion of crops requiring pollination by animals is increasing steadily (Krell et al., 2018; Roubik et al., 2018). Insects contribute to the pollination of about 75% of the crop species, for food (seeds and fruits), fibre and biofuels. Evaluating the dependency on insect pollination of a crop or of a new cultivar constitutes a crucial step to ensure sufficient yield (Gallai et al., 2009). Methods to evaluate such dependency are diverse, rarely comparable and often incomplete. Some studies are performed in small plots whereas others concern fields of several hectares (Stanley et al., 2013; Westcott and Nelson, 2001). Observations are conducted in greenhouses or in the field (Willmer, 2011), on open or on caged plants (Pierre et al., 2009; Steffan-Dewenter, 2003). Yield is assessed with different parameters (fruit set, seed set, seed oil content, seed weight) on different parts of the plants (from only several flowers to entire plants) or on total yield (tonnes) per hectare (Bartomeus et al., 2014; Blochtein et al., 2014; Free, 1993; Gallai et al., 2009; Krell et al., 2018; Roubik et al., 2018). For example, pollination dependency can be estimated at the flower and insect scales, recording parameters such as the number of pollen grains transferred per visit, pollen viability or pollen tube growth, or, for an agronomic point of view, the final yield has to be estimated at a field scale.

A comparison of all these approaches and methods is therefore required to propose the most appropriate ones. We chose to focus our survey on methods tested with oleaginous oilseed rape because its pollination dependency is still under debate (Carrington, 2013; Garibaldi et al., 2016; Lindström et al., 2015; Marini et al., 2015; Pierre and Renard, 2010; Potts et al., 2016). Several authors claimed the complete dependency to insect pollination whereas others estimated the dependency to be very low due to wind or to autonomous self-pollination (Delaplane and Mayer, 2000; Gallai, 2008; Ouvrard et al., 2017; Witter et al., 2014).

Oilseed rape, or canola (*Brassica napus* L. *oleifera*, Brassicaceae), is widely cultivated worldwide (FAOSTAT, 2016) (Fig. 1).

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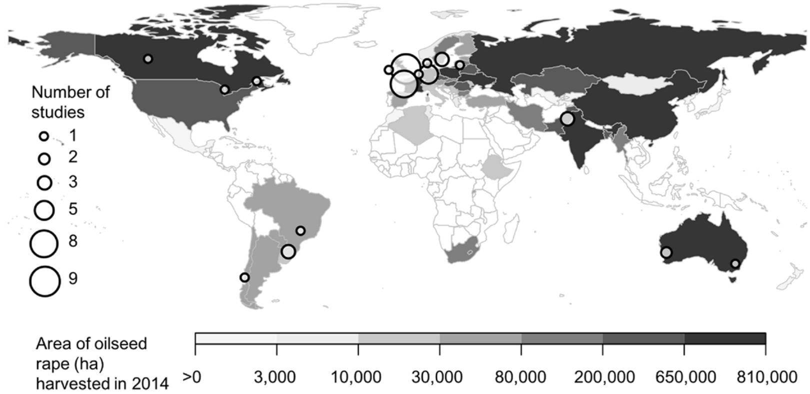

Fig. 1. Areas of oilseed rape worldwide cultivation in 2014 (data from FAOSTAT, 2016) and the number of studies dedicated to oilseed rape pollination (1956–2018).

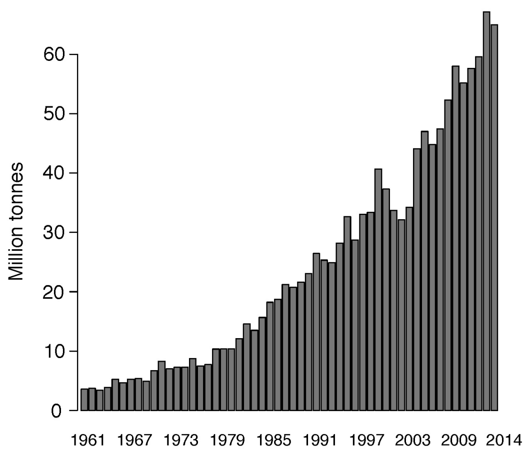

Fig. 2. The worldwide evolution of oilseed rape production (in million tonnes) from 1961 to 2014 (data from FAOSTAT, 2016).

Oilseed rape production has increased considerably during the past 50 years (Fig. 2). With 35.7 million ha, oilseed rape is the third most cultivated oleaginous crop and represents 16% of oil production worldwide (Fig. 3A) (FAOSTAT, 2016). In the European Union, oilseed rape is the most productive oleaginous crop (24.4 million tonnes/year), representing 55% of oleaginous production (Fig. 3B) (FAOSTAT, 2016). The increase in oilseed rape production is recent, with production having risen from 3.6 million tonnes in 1961 to 65 million tonnes in 2014 as a result of improvement in oil quality (FAOSTAT, 2016, no data from FAO before 1961; Fig. 2). Oilseed rape production is still increasing as a result of policy support for biofuels. Since the 2000s production has multiplied six-fold worldwide (to 1,901,000 barrels a day) and by 14 times in the European Union (EU) (EIA, 2016). Biofuel from oilseed rape represents 79% of biofuel production in EU and 13% in the United States (Ajanovic, 2011).

Several modes of pollination occur in *B. napus*. The floral morphology seems adapted to insect pollination, with accessible open, bright-yellow flowers, high volume (up to 6 μL/flower) of sugar-rich nectar, and sticky pollen (Blochtein et al., 2014). Oilseed rape flowers are abundantly visited by insects, especially honeybees (*Apis mellifera,* Delaplane and Mayer, 2000; Delbrassinne and Rasmont, 1988; Halinski et al., 2015; Kirk and Howes, 2012; Westphal et al., 2003; Witter et al., 2014). As a result, since the Second World War, *B. napus* has been considered the most important plant for honey production (Calder, 1986; Delaplane and Mayer, 2000; Kirk and Howes, 2012; Westcott and Nelson, 2001). Insects seem to be particularly effective pollinators of this crop, as it is regularly cited in the literature as suffering reduced yield as a result of pollinator decline (Carrington, 2013; Corbet et al., 1992; European Commission, 2015a; Garibaldi et al., 2016, 2009, Potts et al., 2014, 2016).

Wind pollination is another potentially significant mode of pollination for *B. napus* although the oilseed rape flower morphology is reducing the chance of wind pollination (Cresswell et al., 2004). In several studies, airborne pollen resulted in high pollen deposition in the field (Hayter and Cresswell, 2006) and high fruit set (Pierre et al., 2009; Williams, 1984). The wind not only is an effective pollen vector carrying pollen from plant to plant but also can induce direct mechanical contacts between flowers or provoke pollen deposition within a single flower. Under greenhouse conditions, the effect of wind has been

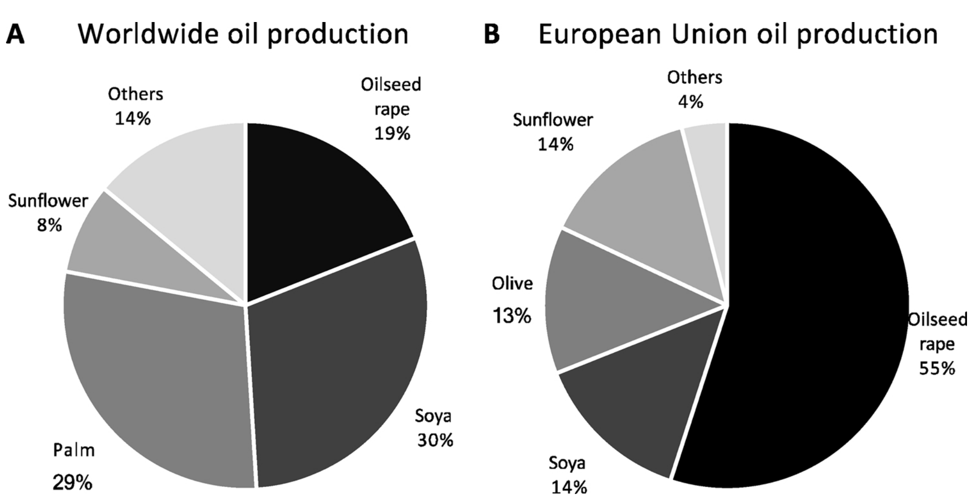

Fig. 3. Worldwide and European Union main oil crop production in 2014 (data from FAOSTAT, 2016).

simulated by shaking the plants twice a day, resulting in seed yield similar to that resulting from hand pollination (Eisikowitch, 1981; Williams et al., 1986).

The benefits provided by insect compared to wind pollination are not known with certainty, especially for the most recently developed cultivars (Hayter and Cresswell, 2006; Jauker and Wolters, 2008; Klein et al., 2006; Morandin and Winston, 2005; Pierre and Renard, 2010). Spontaneous self-pollination, without either wind or insects, seems increasingly important in newer varieties (Ouvrard et al., 2017). Gallai (2008) considered *B. napus* to be moderately pollinator-dependent, with 10–40% of yield depending on insects. Some studies have concluded that insect pollination has no effect on yield (Hudewenz et al., 2014; Langridge and Goodman, 1982; Lindström et al., 2015; Marini et al., 2015; Mesquida et al., 1988), whereas others have shown a strong effect of insect pollination (Munawar et al., 2009). In consequence, it is unclear how yield depends on insect pollination. The question is complicated by the fact that field constraints and protocols influence the plant physiology, the efficiency of pollination, and the seed yield.

Landscape characteristics, i.e. field size and presence of semi-natural habitats as hedges or meadows, influence pollinator abundance, diversity and pollination services provided to crops (Bartomeus et al., 2015; Connelly et al., 2015; Kennedy et al., 2013). The numbers and diversity of oilseed rape visiting insects are influenced by adjacent landscape (Bartomeus et al., 2014; Halinski et al., 2015) whereas landscape context is often poorly described.

However, climatic parameters also strongly influence the diversity of flower-visiting insects (Kleijn and van Langevelde, 2006), as well as plant growth, phenology, and physiology. *B. napus* seed yield is affected by the quality of vernalisation, the sum of the effective temperatures, the temperatures during the flowering period, the day length, the duration of the growing season (de Koning and van Diepen, 1992), and the water stress (Champolivier and Merrien, 1996). Differences in climatic conditions affect both plant physiological parameters (leaf area index, chlorophyll efficiency, flowering period, responses to stress) and biotic interactions (pest infestation, pollinator diversity and abundance). The response to insect pollination probably varies in a pattern similar to the European gradient observed by Leonhardt et al. (2013), whereby crop dependency on insect pollination, insect diversity, and stability of pollination services all increased from the cold Northern to the warm Southern European countries. For example, pollinator dependency is contingent partly on the flowering-period length. The flowering period extends from 20 to 45 days in Europe (Bommarco et al., 2012; Delbrassinne and Rasmont, 1988; Free and Ferguson, 1980; Lerin and Rivault, 1982; Ouvrard et al., 2017; Stanley et al., 2013; Williams, 1984; Williams et al., 1987) and in North America (McGregor, 2009; Morandin and Winston, 2005), but from 56 to 69 days in Australia (Manning and Boland, 2000; Manning and Wallis, 2005) and from 19 to 82 days in Brazil (EMBRAPA, 2016; Tomm et al., 2009). The period of flowering determines insect abundance. Pollinating insect visits have been recorded at higher rates on late-flowering cultivars than on early-flowering ones (Hayter and Cresswell, 2006).

To compare the different methods used and the subsequent results, we conducted a semi-quantitative review of publications explicitly dealing with *B. napus* pollination and production. Our aim was (1) to provide an overview of the current state of research, (2) to classify the diversity of research approaches by identifying clusters of publications that addressed pollination in similar ways, and (3) to highlight some important challenges for the future of research devoted to the analysis of pollinator dependency and pollination modes.

We compared the selected studies in regard to several parameters: (1) the cultivar (winter or spring cultivars); (2) the insects monitored and the methods used to evaluate their pollination efficiency; (3) the observation protocol (open or caged); (4) the field conditions (pest pressure, pesticide treatments, soil characteristics, plot size), and (5) the yield estimation methods used.

Finally, we provide recommendations for reliable future studies of *B. napus* pollination and estimation of pollinator dependency for other crops.

2. Material and methods

We conducted comprehensive searches in Google Scholar, Scopus, and ISI Web of Science using the search terms "*Brassica napus*" AND "pollination" AND "yield" to identify existing literature dealing specifically with oilseed rape pollination. We focused on peer-reviewed literature strictly related to *B. napus* and pollination and published between 1956 and 2018. We dismissed papers referring only to gene flow or crossing or to specific hybrid seed production. We retained 46 publications for in-depth analysis (Appendix 1). Despite the worldwide repartition of *B. napus* crop, a majority (70%) of the studies matching our screening has been conducted in European countries (Fig. 1). Our analysis and comparisons were therefore mainly performed on European cultivars and with European results.

We investigated the methods used across the different papers in our dataset, comparing how the field observations were designed, which yield parameters were assessed, and how the pollination vector efficiency was recorded. We focused on the plant material studied (i.e. cultivar, part of the plant evaluated), the field conditions (i.e. field size, plant location within the field), and the parameters used to assess seed production (i.e. fruit set, seed set, seed weight).

3. Results

3.1. Influence of cultivar

Cultivars differ in yield potential, seed quality, and stress tolerance. Oilseed rape cultivars have evolved considerably over the last 35 years thanks to genetic selection. In 2015, the European Agricultural species catalogue comprised 1331 then-current cultivars and 953 cultivars no longer in use (European Commission, 2015b). Moreover, numerous new cultivars are developed each year. The vast majority (86%) of cropped cultivars in 2015 were winter cultivars, with spring cultivars being less prevalent (187 out of 1331; European Commission, 2015b). The literature reflects this imbalance to a degree, as 10 of the studies we examined were performed on spring cultivars and 31 on winter cultivars.

Each cultivar has particular properties of attractiveness to and dependency on pollinators, mainly due to nectar volume, total sugar concentration (Blažytė-Čereškienė et al., 2010; Kevan et al., 1991; Pierre et al., 1999) and sugar and amino acid composition (Bertazzini and Forlani, 2016). In the studies we assessed, nectar volume varied from 0.2 to 6 μL/flower per day (Mesquida et al., 1991; Pierre et al., 1999), and total sugar concentration ranged from 8.2 to 66.5%. Nectar concentrations of the main sugars, sucrose, glucose, and fructose, differed among cultivars. Flowering phenology, the quantity of pollen per flower, and the presence or absence of a self-incompatibility system also varied greatly among cultivars (Bertazzini and Forlani, 2016; Lindström et al., 2015; Marini et al., 2015; Olsson, 1960). However, such information is not officially available to farmers and maybe not adequately considered by seed developers.

It is particularly important to note the presence of cytoplasmic male sterility because male-sterile cultivars produce no pollen and are strictly dependent on pollen transfer from a male-fertile cultivar. Of the 11 studies on spring oilseed rape, ten were performed on fully fertile cultivars (Bartomeus et al., 2014; Becker et al., 1992; Blažytė-Čereškienė et al., 2010; Bommarco et al., 2012; Jauker et al., 2012; Jauker and Wolters, 2008; Kevan and Eisikowitch, 1990; Sabbahi et al., 2005; Stanley et al., 2013; Williams et al., 1986), while the last one investigated both male-fertile and male-sterile cultivars (Jauker et al., 2012). Only two studies (Stanley et al., 2013; Williams et al., 1986) compared fully fertile spring cultivars with fully fertile winter cultivars. Of the 31 winter oilseed rape studies, 23 were performed on fully fertile cultivars, and six on both fully fertile and male-sterile cultivars

(Diepenbrock, 2000; Mesquida and Renard, 1981, 1982; Pierre et al., 2009).

Across all papers we explored, one cultivar, 'Jet Neuf', was studied in different countries, by different teams, and during several years (Delbrassinne and Rasmont, 1988; Lerin and Rivault, 1982; Mesquida et al., 1988; Williams, 1984; Williams et al., 1987). For most studies, however, the specificities of the cultivar studied are not stated (Marini et al., 2015; Sabbahi et al., 2005). The year the study was performed is generally the only information available to help to identify the cultivar group involved (but see Bertazzini and Forlani, 2016; Lindström et al., 2015). Given this diversity of cultivars, comparisons among studies could be inaccurate due to the high variability among cultivars.

3.2. *Effects of insects monitored and monitoring approaches*

3.2.1. *Monitored insect species and oilseed rape cultivars*

Two different approaches have been developed to assess insect pollination: observational approaches monitoring insects present in the field and experimental approaches monitoring managed insects within cages or excluding insects with bagged plants. For oilseed rape, the managed species most frequently used is the honeybee (*Apis mellifera*). Honeybees were used in 90% of the studies we assessed that involved managed insects (Table 1).

The effects of honeybees on oilseed rape yield differed greatly among studies, from non-significant (Lerin and Rivault, 1982) to a five-fold increase in yield (Munawar et al., 2009). Variations in the environmental conditions, methods and cultivars used can explain such differences. Recording insects only in terms of their presence or absence or the number of visits does not estimate real pollinator effectiveness, which also depends on insect behaviour (contacts with reproductive organs, time per flower, number of flowers visited) (Willmer and Stone, 2004). Although this information is time-consuming to record, it is more precise and hence necessary.

Notably, honeybees have been described as ineffective visitors because in 88% of visits they do not touch the flower reproductive organs when collecting nectar (Willmer, 2011). Several other insect species, such as solitary bees, bumblebees and hoverflies, are more efficient pollinators of oilseed rape (Kremen et al., 2002, 2007; Rader et al., 2015). On oilseed rape, solitary bees (*Andrena* spp., *Osmia* spp.) are the most efficient, with 71% of visits resulting in pollen deposition to the stigmas (Woodcock et al., 2013). In consequence, several different insect visitor species together increase pollination quality and fruit set (Garibaldi et al., 2013).

The insect pollination dependency differs among cultivars (Hudewenz et al., 2014; Williams, 1978). However, the only three publications related to the same cultivar (Jet Neuf) failed to find any insect visit effect for honeybees, bumblebees or flies (Lerin and Rivault, 1982; Mesquida et al., 1988; Williams et al., 1987).

3.2.2. *Monitoring approaches*

3.2.2.1. Observational approaches. Several methods of insect observations have been used: transect walk, sweeping net catching, pan trap, and fixed-time observation of small plots. Surface area, duration, and time of day also differed among publications. For transect observations, for example, both the size of transect (from 4 to 300 m^2) and the duration of observation (5–15 min, when timed) varied. In consequence, the studies do not provide similar and easily comparable estimates of insect effectiveness (Gibson et al., 2011; Musser et al., 2007; Titmarsh et al., 1991; Westphal et al., 2008).

Observational studies monitoring honeybees in the field reported low bee densities on *B. napus* flowers (Ouvrard, 2018; Ouvrard et al., 2017). Westcott and Nelson (2001) observed 1 honeybee/100 m^2/h on male-sterile flowers but 20 honeybees/100 m^2/h on fully fertile flowers. From nine to 360 honeybees/100 m^2/h were recorded depending on the hive density in the vicinity of the fields (Sabbahi et al., 2005). Such densities were low compared to experimental studies with caged plants.

Table 1
Numbers, types, and pollination effectiveness of managed insects used in experiments on caged oilseed rape plants (numbers in brackets represent estimates of workers per hive).

Number of honeybees used	Other insects	Caged area (m^2)	Conclusion about insect pollination	Reference(s)
One colony (around 40,000 workers)	–	9	No effect	(Mesquida et al., 1988)*
–	Two *Bombus terrestris* queens (founder)	9	No effect	
–	Several hundred *Calliphora* flies	9	No effect	
One colony (around 40,000 workers)	–	12.5	Positive effect on seed quantity No effect on seed oil content and germination	(Adegas and Nogueira Couto, 1992)
One colony (around 40,000 workers) with access to both the cage and the outside	–	9	No effect on seed quantity	(Free and Nuttall, 1968)
One small colony (around 10,000 workers)	–	7.3	Variable effects	(Williams et al., 1987)*
One small colony (around 10,000 workers)	–	9	No effect on fully fertile plants	(Pierre et al., 2009)
One small hive (around 5000 workers), no queen	–	9	No effect	(Mesquida and Renard, 1981)
500 workers	–	4 (5 plants)	Positive effect on seed quantity	(Munawar et al., 2009)
250 g (around 3250 workers)	10 *Osmia* sp.	7.5	Positive effect on seed quantity	(Steffan-Dewenter, 2003)
–	0 to 100 *Osmia* sp.	7.5		
Honeybees outside the cages, 17 hives for 2.7 ha	–	4	No effect	(Langridge and Goodman, 1982)
Approximately 200	–	7.5	Positive effect on seed quantity	(Jauker et al., 2012)
–	1 to 36 *Osmia rufa*	7.5		
–	1 to 96 *Eristalis tenax* and *Episyrphus balteatus*	7.5		
–	12 and 25 *E. balteatus*	4	No effect	(Jauker and Wolters, 2008)
–	One *Bombus* sp. queen (founder)	4 (16 plants)	No effect on seed quantity	(Lerin and Rivault, 1982)*

* Studies using the same *B. napus* cultivar, Jet Neuf.

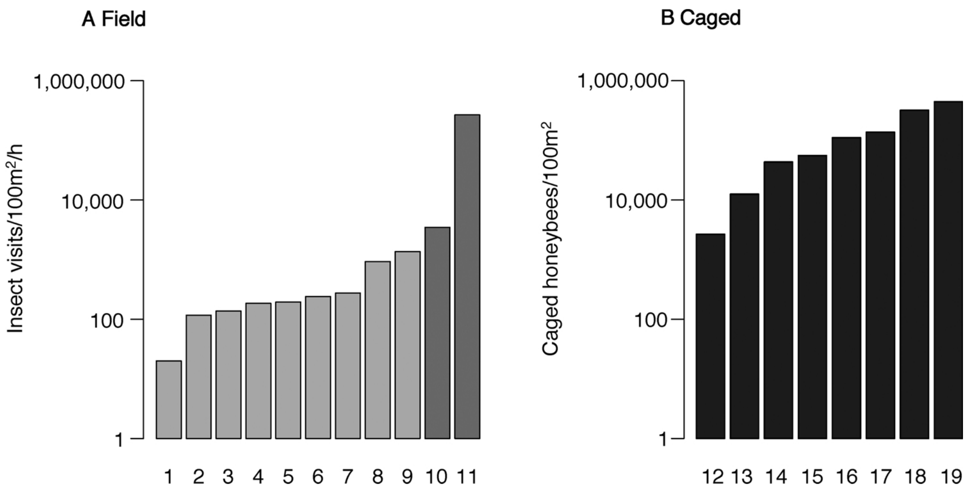

Fig. 4. Recorded numbers of flowers visited by insects in observations performed under field conditions and numbers of insects introduced in experimental caged conditions. (**A**) Visits by all insects under field conditions, standardised per 100 m^2 and hour, in large fields (> 10 ha, light grey) and in medium-sized plots (< 0.5 ha, grey). (**B**) Numbers of honeybees with caged plants, standardised per 100 m^2 (black). Each bar provides data (median) from one of the following publications: 1.(Westcott and Nelson, 2001) 2.(Morandin and Winston, 2005) 3.(Blažytė-Čereškienė et al., 2010) 4.(Sabbahi et al., 2005) 5.(Lindström et al., 2015) 6.(Bartomeus et al., 2014) 7.(Ouvrard et al., 2017) 8.(Bartomeus et al., 2015) 9.(Stanley et al., 2013) 10.(Brunel et al., 1994) 11.(Ali et al., 2011) 12.(Jauker et al., 2012) 13.(Munawar et al., 2009) 14.(Steffan-Dewenter, 2003) 15.(Mesquida and Renard, 1981) 16.(Pierre et al., 2009, 2002) 17.(Williams et al., 1987) 18.(Adegas and Nogueira Couto, 1992) 19.(Free and Nuttall, 1968; Mesquida et al., 1988).

Table 2
Bagged or caged experiments: mesh sizes and effects taken into consideration in the different studies (ND: No data specified).

Mesh size (material)		Main objective(s) of bagging or caging	Secondary mesh effect(s) recorded	Reference
Bags	2 mm (ND)	No pollinator access Keeping managed insects inside or outside Allowing pollen flow	Wind speed decrease	(Pierre et al., 2009)
	1.2 mm (tulle)	No pollinator access	None mentioned	(Stanley et al., 2013)
	1 mm (tulle)	No pollinator access	None mentioned	(Bommarco et al., 2012)
	ND	No pollinator access	None mentioned	(Blochtein et al., 2014)
	(Butter paper)	No pollinator access	None mentioned	(Ali et al., 2011)
Cages	2.5 mm (ND)	No pollinator access	No effect on airborne pollen flow	(Langridge and Goodman, 1982)
	2 mm (plastic cloth)	No pollinator access Keeping managed insects inside	Wind speed decrease of 90% for wind of 2.75 km/h and of 60% for wind of 4.50 km/h	(Mesquida et al., 1988*; Mesquida and Renard, 1981)
	2 mm (monofilament synthetic cloth)	No pollinator access	None mentioned	(Mesquida and Renard, 1982)
	1 and 2.5 mm (white polypropylene)	No pollinator access	Possible effect on temperature and solar radiation	(Durán et al., 2010)
	0.74 × 1.12 mm (polyethylene)	No pollinator access	No effect on wind	(Sutter and Albrecht, 2016)
	1 mm (plastic transparent net)	No pollinator access	Minor effects to micro-climatic conditions	(Marini et al., 2015)
	1 mm (plastic gauze)	No pollinator access Keeping managed insects inside	None mentioned	(Jauker et al., 2012; Jauker and Wolters, 2008)
	< 1 mm (plastic gauze)	No pollinator access Keeping managed insects inside	None mentioned	(Steffan-Dewenter, 2003)
	0.7 mm (14 meshes/cm) (ND)	Keeping managed insects inside or outside	Wind speed decrease Potential greenhouse effect	(Lerin and Rivault, 1982)*
	Only small insects (e.g. thrips and midges) could pass (tygan mesh)	No pollinator access Keeping managed insects inside	None mentioned	(Williams et al., 1987)*
	ND	No pollinator access Keeping managed insects inside	None mentioned	(Adegas and Nogueira Couto, 1992; Kevan and Eisikowitch, 1990; Munawar et al., 2009)
	ND	No pollinator access	None mentioned	(Free and Nuttall, 1968; Sabbahi et al., 2005; Shakeel and Inayatullah, 2013)

* Studies using the same *B. napus* cultivar, Jet Neuf.

In consequence, observations performed in the field with wild insects showed highly variable but generally low flower visitation rates (Fig. 4A), ranging from 60 to 1300 flowers visited/100 m^2/h (Bartomeus et al., 2015, 2014; Blažytė-Čereškienė et al., 2010; Mesquida et al., 1988; Morandin and Winston, 2005; Stanley et al., 2013).

On the other hand, studies conducted on medium-sized plots (100–150 m^2) showed high numbers of flowers visited by insects (Fig. 4A). In France, high numbers of visits (extrapolated to 3480 flowers visited /100 m^2/h, including 1560 by honeybees) on walked transects have been recorded (Brunel et al., 1994). In Pakistan, an extremely high rate of 0.7 insect visits/flower/minute (can be extrapolated to 267,120 flowers visited/100 m^2/h) has been recorded (Ali et al., 2011). The enormous attractiveness of the medium-sized patches of oilseed rape in the context of the Pakistanis experimental station might explain such high numbers. Considering insect visitation rate on a field scale is therefore more realistic to estimate insect dependency.

3.2.2.2. Experimental approaches. Honeybees were the most used insects for experimental approaches. Over 12 studies, 10 were conducted with honeybees (including two studies with both honeybees and other insects), and two were conducted only with non-honeybee pollinating insects (Table 1).

The majority of the experimental studies conducted with managed honeybees on caged plants used very high insect densities, up to 400,000 times higher than those observed in open fields (Table 1, Fig. 4B, but see Mesquida and Renard, 1981). Oilseed rape pollination by managed species other than honeybees has been little studied, and only with low insect densities, comparing few wild insects to several thousands of honeybees (Steffan-Dewenter, 2003). Lerin and Rivault (1982) worked with *Bombus terrestris* and did not detect any significant seed yield increase. Mesquida et al. (1988) compared the pollination efficiency of *Apis mellifera*, *B. terrestris*, and *Calliphora* spp. and they did not detect any significant increase in seed yield (Table 1). The effects detected differed greatly among insect species and methods (Witter et al., 2015). Nearly half of the studies (six out of 13) detected no effect or even a negative effect of insect visitors on final seed yield despite insect densities being higher under cages than in open field conditions (Fig. 4B).

The cages or bags used to manage insects influenced the observations and can constitute a less favourable environment for the plants (Free, 1993; Olsson, 1960). Insect pollination studies commonly use bags and cages (screen tents) made of fine mesh (up to 2.5 mm) (Kearns and Inouye, 1993; Shivanna and Tandon, 2014). Mesh cages modify microclimatic conditions (temperature, Kearns and Inouye, 1993) and duration of flowering (Marini et al., 2015). In plant species that are partly wind pollinated, such as oilseed rape, the use of a mesh bag is problematic because it modifies wind velocity (Table 2). Yields were 11 and 51% lower, respectively, in plots caged with a mesh of 1-mm and 2.5-mm mesh sizes respectively, compared to the yield in open plots observed in the same field (Jauker and Wolters, 2008). The mesh size undoubtedly influenced the effect of wind pollination, even though the consequences of changes in airborne pollen kinetics are difficult to evaluate (Mesquida et al., 1988).

Despite the potential importance of wind pollination (Free, 1993; McCartney and Lacey, 1991; Williams, 1984) and the possible impact of mesh size on wind pollination quality (Gonzalez et al., 1998), only very few studies have taken into consideration the effects of mesh size on wind pollination (Table 2). Pollination rates may be lower inside cages as a result of differences in wind, light, and humidity conditions (Olsson, 1960). It is difficult to separate the effects caused by the absence of insects from those caused by changes in micro-environmental conditions in the cages or inside the bags (Mesquida et al., 1988; Williams et al., 1987).

Caging reduced yield by 30%–50% compared to un-caged field plots (Mesquida et al., 1988; Sabbahi et al., 2005). The cage effect is not compensated by the presence of managed insects. As oilseed rape is considered to be partly wind-pollinated, the estimations of insect dependency are more realistic on un-caged plants.

3.3. Field conditions

3.3.1. Soil characteristics

Soil characteristics (i.e. soil type, soil depth, and nutrient availability, Doran et al., 1994), fertilisation and tillage practices (Sarkar et al., 2007), and previous crops in the crop rotation (Rathke et al., 2005) influence plant growth and final yield. These parameters affected plant development (Sidlauskas and Bernotas, 2003), flower production and floral resources (pollen and nectar) (Kenoyer, 1917), and behaviour, diversity and abundance of pollinators and insect pests (Henry et al., 2012; Kazda et al., 2015; Thompson, 2003; Veromann et al., 2014). They also affected disease pressures (Strehlow et al., 2014) and seed production in regard to both quality and quantity (Cardoza et al., 2012; Hokkanen, 2000; Marini et al., 2015; Ozer, 2003; Rathke et al., 2005, 2006; Sieling and Christen, 1997). Fluctuations in nutrient availability both among and within fields (Cambardella et al., 1994; Miao et al., 2006) affected the yield and modified the pollinator effect (Marini et al., 2015). For some oilseed rape cultivars, nitrogen fertilisation (up to 200 kg/ha) increased seed yield from 49 to 94% (Mahli et al., 2007; Rathke et al., 2006). The gains in seed yield due to insect pollination were directly dependent on the level of nitrogen fertilisation, as the yield increase due to insect pollination was high in plots without any nitrogen input but insignificant with a nitrogen input of 170 kg/ha (Marini et al., 2015). Such yield increases due to fertilisation were higher than the relative contribution attributed to insect pollination (10 to 40%, Gallai, 2008). Nevertheless, soil characteristics were rarely specified or considered in the pollination studies (Cardoza et al., 2012; Marini et al., 2015).

Several studies were conducted under partly or entirely controlled conditions to reduce the influence of soil differences. For instance, some experiments were performed in the field but with potted plants (Lerin and Rivault, 1982). Other studies were conducted in greenhouses (Eisikowitch, 1981; Williams, 1978; Williams et al., 1986) to control additional parameters such as wind and water availability. These methods increase repeatability and improve comparisons within and among studies, whereas they are not commonly used and differ from real field conditions.

3.3.2. Pest infestation and chemicals used

Pollen beetles, mainly *Brassicogethes aeneus* and *Brassicogethes viridescens* (Meligethinae), are the primary pests destroying oilseed rape bud flowers and flowers (Mason et al., 2003; Ouvrard et al., 2016). They reduced both plant fitness and pollinator visitation rate (Alford, 2003; Bartomeus et al., 2015; Veromann et al., 2006). Pollen beetles, and especially the florivorous larvae, decrease the numbers of flowers available to pollinating insects and flower attractiveness. Moreover, pollen beetle infestations increase the numbers of non-legitimate flower visits by bees, decreasing the effectiveness as bees visit flowers without touching the stigmas (Lindström et al., 2018). However, the small size of pollen beetles makes them hard to keep out of the plants. Moreover, pollen beetles have been considered to be effective pollinators, especially in heavily infested fields (Bartomeus et al., 2015). The final effect of pollen beetles results from the balance between the numbers of flowers damaged and the pollination service provided. Such balance seems to be linked to the pollen beetle density that is poorly assessed in studies of oilseed rape insect pollination dependency.

The chemicals used for seed coating and pesticide treatments, both during the study year and in previous years (for persistent compounds), influenced insect behaviour, diversity, and density (Henry et al., 2012; Thompson, 2003; Woodcock et al., 2016). Kazda et al. (2015) showed that the type of active molecules contained in previously used chemicals significantly influenced the bee visitation rates. Nevertheless, seed coating and phytochemical treatments were rarely assessed. Even the use of chemicals during the studied flowering period was generally not discussed. In most instance, no information was provided to evaluate any effects of chemicals on pollinator behaviour and the subsequent impact on the yield.

3.3.3. Plot size and shape

At the landscape scale, mass flowering crop such as *B. napus* positively impact bee (*Bombus*) densities (Westphal et al., 2003). The size, shape and location of the study plot directly affected plant morphology and physiology (Otypková and Chytry, 2006), insect visits (Garibaldi et al., 2016; Olsson, 1960; Prasifka et al., 2005), wind velocity (Klein et al., 2006) and final yield (Arny, 1921). Field size conditioned both insect visits and insect movements within the field (Le Féon, 2010). Insect visitors were more diverse and numerous at the field edges than in the field centre, increasing pollination success at the edges (Brunel et al., 1994). The pollination quality depended primarily on insect density in fields smaller than 2 ha and on insect diversity in fields larger than 20 ha (Garibaldi et al., 2016). In consequence, data from small plots cannot be extrapolated to large fields. Comparisons among studies have to consider the size of the plot or of the field studied (Table. 3).

Field sizes differed greatly from one study to another, as well as

Table 3
Types and sizes of the experimental plots or fields, and size of the samples used for yield estimations.

Type of studied area	Mean sown area (m^2)	Studied plot size (m^2)	Sample size for yield estimation (per replicate and per treatment)	Reference
Experimental plot	0.24	0.24	16 plants	(Lerin and Rivault, 1982)
	1.50	1.50	10 plants	(Mesquida and Renard, 1981)
	4.00	4.00	All plants	(Langridge and Goodman, 1982)
	7.30	7.30	10 to 50 plants	(Williams et al., 1987)
	7.50	7.50	5 plants	(Steffan-Dewenter, 2003)
	9.00	9.00	50 main racemes	(Pierre et al., 2009)
	10.00	0.08	–	(Brunel et al., 1994)
	12.00	12.00	100 flowers	(Adegas and Nogueira Couto, 1992)
	12.00	2.00	5 plants for fruit set 100 fruits for seed set	(Munawar et al., 2009)
	27.00	2,25	All plants	(Jauker and Wolters, 2008)
	45.00	4.00	20 fruits for seed set 100 seeds for seed weight	(Shakeel and Inayatullah, 2013)
	57.00	1.90	10 plants	(Jauker et al., 2012)
	100.00	9.00	All plants	(Free and Nuttall, 1968)
	100.00 to 400.00	100.00 to 400.00	200 to 300 plants	(Becker et al., 1992)
Commercial field	1800 ± 0	9.00	All plants	(Mesquida and Renard, 1982)
	4000 ± 0	4000.00	30 plants	(Ali et al., 2011)
	150,000 ± 55,000	2.00	All plants on 1 m^2	(Durán et al., 2010)
	110,000 ± 60,000	1250.00	20 plants	(Witter et al., 2014)
	110,000 ± 66,000	110,000 ± 66,000	The 40 first flowers of the main raceme of 18 plants	(Ouvrard et al., 2017)
	123,000 ± 116,000	1250.00	10 plants	(Bommarco et al., 2012)
	139,000 ± 47,000	200.00	All plants on 50 m^2	(Lindström et al., 2015)
	around 270,000	200.00	20 plants	(Free and Ferguson, 1980)
	560,000 ± 170,000	6.00	6 flowers on 18 plants	(Morandin and Winston, 2005)
	1,000,000 ± 0	1.00	All plants	(Manning and Boland, 2000)
	2,590,000 ± 480,000	1.00	All plants	(Manning and Wallis, 2005)

within studies, extending from only a few square meters (Adegas and Nogueira Couto, 1992; Steffan-Dewenter, 2003) to 293 ha (Manning and Wallis, 2005). The number of replicates also varied among studies, from one (Manning and Boland, 2000; Mesquida and Renard, 1982; Williams, 1984) to ten fields (Bommarco et al., 2012; Free and Ferguson, 1980; Stanley et al., 2013). A larger number of fields resulted in a greater diversity of field sizes (i.e. from 1 to 40 ha, Bommarco et al., 2012) so that data from multi-field studies reflected a mixture of effects linked to field size.

Independently of plot size, the location within the plot of the plants studied can also strongly influence the results (Arny, 1921). Light and wind conditions, water and nutrient availability, and accessibility to pests and pollinators can all vary from the edge of a plot to its centre (Cromartie, 1975). Different studies used different protocols: studying plants at a given distance from the edge, plants from the whole plot, plants at the centre of the field or plot (to avoid edge effect), or random plants in the plot. Different field plots should be considered, from the edge to the centre to appreciate pollinator effects over an entire field.

3.4. Yield estimation

Because of economic considerations, the final yield constitutes the best criterion for estimating pollination success (i.e. fruit set, seed set, seed weight, oil content). Yield estimates per hectare provide the most useful information for both farmers and seed companies. The accuracy of these estimates has been a subject of debate (e.g., Diepenbrock, 2000). From an economic point of view, the most useful parameters to estimate are seed weight production per area and seed quality. High seed quality refers to high oil content and low chlorophyll content. For spring cultivars, insect pollination led to higher oil and lower chlorophyll contents, increasing the market value by 20% (Bartomeus et al., 2014; Bommarco et al., 2012). In contrast, studies with winter cultivars reported no effect of insect pollination on seed oil content (Adegas and Nogueira Couto, 1992; Langridge and Goodman, 1982; Williams et al., 1987). Two parameters were particularly variable among studies, the seed ripeness stage and the plant section used.

3.4.1. Seed ripeness stage

Seed composition changes over the time from fertilisation to seed maturity, mainly with respect to water and oil contents (Norton and Harris, 1975). Seed abortion occurs from two weeks after the end of flowering to seed maturity (Clarke, 1979), reducing seed numbers by 30% (Norton and Harris, 1975). Comparing seed production based on data collected at different maturity stages could therefore confound estimates of pollinator impact on final seed yield.

The time of seed harvest differed greatly among studies: only 12 days after pollination (Morandin and Winston, 2005), after three to five weeks (Norton and Harris, 1975), or after six or eight weeks when the seeds are mature (Stanley et al., 2013).

Moreover, mature seeds could differ in water content. In most of the studies, freshly harvested plants were evaluated without indication of the seed water content (but see Rathke et al., 2005). Drying protocols also differed among studies: four weeks at 25–30 °C (Steffan-Dewenter, 2003), 12 h at 25 °C (Jauker et al., 2012), room temperature for an unspecified time (Stanley et al., 2013), or one week in a greenhouse followed by 24 h at 65 °C (Marini et al., 2015).

3.4.2. Compensatory mechanisms

In oilseed rape plants, undeterminate inflorescences and multiple compensatory mechanisms influence final yield assessed as fruit set, seed weight, seed size or seed numbers (Durán et al., 2010). The observed parameters used to assess seed production differed among studies (Table 4).

Insect pollination effects differed depending on the section of the plant (Mesquida et al., 1988) and the position of the ramification considered (Clarke, 1979). The most productive flowers, i.e. those with highest fruit set, seed set, and seed weight, were found on the lower half of the main raceme and provided 72–81% of the plant total seed production (Clarke, 1979; Diepenbrock, 2000; Tayo and Morgan, 1975). For example, insect pollination increased the seed weight by 11% when only the first 25 flowers were considered, and by 4% when the first 50 flowers of the main raceme were considered (Mesquida et al., 1988).

The plant sections studied, and the number of flowers assessed differed greatly among studies. Most of the papers took whole plants into consideration to evaluate the seed yield parameters (Bartomeus

Table 4
Observed yield parameters.

	Parameters		References
Seeds	Size		(Manning and Boland, 2000)
	Quality	Germination rate	(Kevan and Eisikowitch, 1990; Langridge and Goodman, 1982)
		Oil content	(Adegas and Nogueira Couto, 1992; Langridge and Goodman, 1982; Williams et al., 1987)
		Oil and chlorophyll contents	(Bartomeus et al., 2014; Bommarco et al., 2012)
	Weight	Per individual seed	(Adegas and Nogueira Couto, 1992; Lerin and Rivault, 1982; Williams et al., 1987)
		Per fruit	(Blažytė-Čereškienė et al., 2010; Blochtein et al., 2014; Manning and Boland, 2000; Stanley et al., 2013)
		Per plant	(Bartomeus et al., 2014; Blochtein et al., 2014; Mesquida et al., 1988; Steffan-Dewenter, 2003; Williams, 1978; Williams et al., 1987; Witter et al., 2014)
		Per thousand seeds	(Durán et al., 2010; Mesquida et al., 1988; Mesquida and Renard, 1981; Sabbahi et al., 2005; Shakeel and Inayatullah, 2013)
		Per plot	(Free and Nuttall, 1968; Halinski et al., 2018; Marini et al., 2015; Mesquida and Renard, 1982; Mesquida et al., 1988; Williams et al., 1986)
Fruits	Per plant		(Blochtein et al., 2014; Jauker et al., 2012; Mesquida et al., 1988; Pierre et al., 2009; Williams et al., 1986)

et al., 2014; Bommarco et al., 2012; Durán et al., 2010; Free and Nuttall, 1968; Lerin and Rivault, 1982; Manning and Boland, 2000; Manning and Wallis, 2005; Williams et al., 1986; Witter et al., 2014). Other studies were performed on three (Morandin and Winston, 2005) or six randomly selected flowers (Stanley et al., 2013), on the first 20 (Williams, 1978) or 50 flowers of the main raceme (Mesquida and Renard, 1981), or on all flowers of the main raceme (Mesquida and Renard, 1981, 1982; Pierre et al., 2009).

Insect pollination increased seed set of individual flowers but not at the plant level (Lerin and Rivault, 1982) and at the plot level, where pollination quality did not seem to be a limiting factor for yield. Such differences are mainly due to compensation effects. Compensation is a complex mechanism of positive plant response to stresses. Oilseed rape shows effective compensation mechanisms at the level of seed yield (Clarke and Simpson, 1978; Diepenbrock, 2000; Lerin and Rivault, 1982; Mesquida et al., 1988; Mesquida and Renard, 1981; Williams and Free, 1979). When plants were adequately pollinated, the flowering period was reduced by a few weeks, along with the stem elongation and the number of ramifications. In consequence, plants were more compact, with more advanced fruit growth and homogenization of seed size and maturity stages (Lerin and Rivault, 1982; Mesquida and Renard, 1981; Williams et al., 1987). When flowers were poorly pollinated or were damaged by pests, their numbers increased to compensate for the loss (Angadi et al., 2003; Diepenbrock, 2000; Marini et al., 2015; Williams and Free, 1979). A low seed number resulted in heavier seeds (Adegas and Nogueira Couto, 1992; Mesquida et al., 1988; Williams, 1978) and greater seed size (Durán et al., 2010; Marini et al., 2015). Likewise, a higher fruit set on the main raceme resulted in a lower number of ramifications and fruits on ramifications (Lerin and Rivault, 1982; Mesquida et al., 1988). Some studies found that a higher number of fruits per plant was partially counterbalanced by a lower number of seeds per fruit (Manning and Wallis, 2005; Sabbahi et al., 2005; Steffan-Dewenter, 2003), whereas others did not find such compensation (Jauker and Wolters, 2008; Shakeel and Inayatullah, 2013).

4. Discussion

Pooling together the main factors determining the yield (pollinator visits, pest attacks, soil fertility) for two close cultivars explained only 20% of the yield variance (Bartomeus et al., 2015). Even if Free and Ferguson (1980) discussed the possibility of application of insecticides to the field borders to prevent or delay the spread of pests throughout the crop, these factors have rarely been taken into consideration in evaluating the impact of pollinating insects on seed yield. Besides insect pollination effects, seed yield was strongly affected by several factors, and their interactive effects (Cardoza et al., 2012), such as the genetic potential of the cultivar and its ability to compensate for damage (Clarke and Simpson, 1978; Diepenbrock, 2000; Lerin and Rivault, 1982; Pavlista et al., 2011; Sana et al., 2003), resource availability (mainly nitrogen and water; Pavlista et al., 2011; Rathke et al., 2006), soil pH (Bartomeus et al., 2015), sowing density, environmental conditions (Angadi et al., 2003; de Koning and van Diepen, 1992; Zajac et al., 2013), and pest pressure (Bartomeus et al., 2015; Brown et al., 1999). Without taking into consideration the effects of these numerous parameters, it is difficult to isolate the proportion of seed yield linked to insect pollination. Numerous parameters and compensation mechanisms affect seed yield and insect pollination dependency. Moreover, the diversity of cultivars and methods used across studies and the moderate number of parameters usually considered make hazardous comparisons among studies.

4.1. Influence of cultivar

Few of the current cropped cultivars are evaluated in scientific studies due to the quick market turnover of cultivars. Because of the diversity and specificity of the responses of different cultivars to spatial and temporal parameters, the most cultivated cultivars have to be studied to evaluate their insect pollination dependency. To facilitate comparisons among studies, information about the type of cultivar used (spring or winter cultivar, hybrid or not, fully fertile or not) and parameters such as plant size, flowering phenology and nectar quantity, are required. Total sugar content and nectar volume are easily evaluated in the field with glass capillary tubes and low volume hand refractometer (Ouvrard et al., 2017). Further, there is a need to study interacting effects between cultivar chosen and management practices on pollination dependency (Lindström et al., 2018). Using the same cultivar under different environmental conditions is also highly recommended.

4.2. Effects of insects monitored and monitoring approaches

Even if other wild insect species were recorded as more effective pollinators for oilseed rape, *A. mellifera* remains the most studied pollinating species. This social species, breed in large colonies (> 40,000 individuals per hive) is very convenient to provide numerous workers, adapted to observational approaches in fields. Nevertheless, experimental approaches considering only small plots and caged plants are poorly adapted to such high numbers of honeybees. Moreover, the fine mesh tissue used for cages or exclusion bags, modifies microclimatic conditions (wind, temperature, solar radiation) and influences final plant growth and reproductive success.

Observations with enclosed managed insects are designed to investigate specific plant-insect interactions and high-density effects but are not suitable for providing data useful for agronomic perspectives, as the insect densities, up to 1111 beehives/ha (extrapolated from Free and Nuttall, 1968 and Mesquida et al., 1988) are unrealistic. Furthermore, high insect densities do not seem to result in a positive effect of insect pollination on seed yield, possibly because flowers are damaged by over-visitation (Atmowidi et al., 2007; Mesquida et al., 1988). Overall, high or ultra-high insect densities are not appropriate to study pollinator effect on yield. Working with moderate insect densities (up to 2000–3000 insect visits per 100 m^2/h) seems more realistic and will allow easier field-level extrapolation of the results (Ouvrard et al., 2017; Stanley et al., 2013). For instance, pollination was equally effective with a low solitary bee density (2.5 to 4.8 insects/m^2) than with a high honeybee density (26.7 insects/m^2) (Jauker et al., 2012).

Monitoring should be conducted with simple, replicable, and standardised methods (Gotelli and Colwell, 2001), i.e. pan traps, transect walk observations and net sampling to record insect diversity (Roulston et al., 2007; Westphal et al., 2008), and observation plots to record flower visitation rates (Fijen and Kleijn, 2017). Observation periods of 20–30 minutes are a usual method, largely used by different researchers in pollination trials (Albrecht et al., 2007; Fijen and Kleijn, 2017; Moquet et al., 2017; Olesen et al., 2008; Ouvrard et al., 2017; Potts et al., 2003; Westphal et al., 2008; Willmer and Stone, 2004). Such period allows recorders to perform several observations a day and to observe during more than a few minutes. We recommend observations of 1 m^2 plots with a known number of open flowers, for 20–30 minutes, repeated at different periods of the day during favourable weather conditions. Control plots with low insect visitation could be obtained by spraying insect-repellent molecules on plants (Free, 1993; Free and Ferguson, 1980; Naumann et al., 1994; Solomon and Hooker, 1989) and could be combined with hand pollination experiments that enable full pollination as a control of the open pollination (to detect any pollen transfer limitation). When cages are used, it is preferable to use a large mesh size (> 2.5 mm) to minimise the decrease of wind velocity. Moreover, to assess the low impact of cages on parameters other than insect visits, measurement of wind velocity and airborne pollen quantity both inside and outside the cages is recommended.

4.3. Field conditions

As for cultivars, field conditions (soil characteristics, field size and location, pest pressure, chemical treatments and fertilization) are diverse and influence plant growth, yield and insect pollination dependency. Besides, information about any chemicals used in the field, and when possible about crops previously cultivated in the same field, should be provided. Performing soil description and soil analysis for nitrogen availability, recording fertilisation management and field management history, and working with plots that are as homogenous as possible are recommended. However, these parameters are poorly described in most of the insect pollination dependency studies, complicating comparisons among the results obtained.

As the small size of pollen beetles makes them hard to keep out of the study plants, even with fine-mesh cages or bags (Shivanna and Tandon, 2014), we recommend the use of classical yellow water traps (Sedivy and Vasak, 2002) to estimate and compare levels of pollen beetle infestation among plots and during different flowering stages (before and during flowering). Even if yellow pan traps do not provide information about where the pollen beetles occur in the plant, the level of pollen beetle infestation can provide clues to assess impacts on pollinating insect visits (Lindström et al., 2018).

The Food and Agriculture Organization (FAO) of the United Nations has published standardised protocols for studying pollinator effects on crop yields (Vaissière et al., 2011). Observations at fixed distances from the field edge are recommended (25, 175, and 325 m for large fields (> 450 m) or 5, 15, 35, and 45 m for small fields, Vaissière et al., 2011). Using these protocols would facilitate comparisons among studies.

4.4. Yield estimation

Yield estimation is the last step providing the economic value for growers. Nevertheless, across the studied papers, harvesting methods, and parts of the plants used (entire plants or plant sections) differed. Moreover, *B. napus* is remarkable by effective compensatory mechanisms occurring at the plant level. These mechanisms notably impact flower, fruit and seed production. Therefore, to estimate the impact of pollination on seed yield under realistic field conditions and between cultivars, we recommend measuring the total seed weight produced for entire plants per unit area (m^2 for example), along with quality parameters (oil and water contents). Global seed yield estimates should take into consideration data from the whole plant to prevent any variation of seed production within the plant. Seed production should be estimated on ripe seeds only. We recommend harvesting whole ripe plants and drying the seeds if necessary to reach a water content corresponding to the optimal storage and standard market-quality seed moisture of 7 to 9% (Canola Council of Canada, 2014; Kasprzycka et al., 2010; United Oilseeds, 2009).

In conclusion, similar insect monitoring protocols, assessment of field characteristics and environmental conditions and total seed yield estimations on entire plants are recommended for any other study about insect pollination dependency.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2018.11.006.

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