The Role of Pollination Services in Seed Production: A review

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Abstract

In the face of declining insect biodiversity, this study reviews the critical role of pollination services in seed production of food crops. Insects, as pollinators, play a fundamental role in the reproductive processes of both wild and domesticated plants, impacting global agriculture. While previous reviews have assessed the influence of pollinators on primary food production, this review extends to seed production, an essential precursor in the agricultural supply chain. Here we add to the existing body of literature by reviewing the dependence on pollination services in seed production for the major crops that are propagated via seeds. We show that out of 47 crops analyzed, 16 essentially depend on pollinators, 19 highly, 2 moderately, 3 little, and 7 crops do not depend on insect pollinators at all. This research highlights the significant and often overlooked role of pollinators in seed production, emphasizing the need for further investigation into the potential consequences of changing pollinator populations on global agriculture and food security. It also underscores the importance of preserving pollinator populations and integrating their contributions into economic assessments and databases.

Keywords: Ecosystem services; Seed production; Pollinator declines; Biodiversity; Dependence ratio; Agriculture

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Introduction

The dramatic decline of insect biodiversity (Hallmann et al. 2017; Seibold et al. 2019) not only alarms the public and science (Cardoso et al. 2020), but also poses a threat to ecosystem services provided by them (Dangles and Casas 2019). Insect pollination is one of the most prominent ecosystem services and plays a key role in the reproduction of both wild (Ashman et al. 2004; Rodger et al. 2021) and domesticated plants (Klein et al. 2007). The potential consequences of changing pollinator numbers on agricultural production have been analyzed by various studies, investigating for example effects on crop quality (Klatt et al. 2014), protein content (Fijen et al. 2021), yield stability (Hünicken et al. 2021) and economic welfare (Lippert et al. 2021). Klein et al. (2007) provided an overview of the dependence of crops on pollinators. Their study focused on the primary production of agricultural produce, i.e. the production of plant parts that are produced for direct or indirect human consumption. The role of pollinators in other production systems, like seed production, was not covered by their analysis. The carrot (*Daucus carrota*) for example, does not depend on pollinators directly to produce its taproot (Klein et al. 2007), which is then used for human consumption, but its flowers might depend on pollinators to produce seed, needed for propagation of the crop. With this study we aim to fill this gap, which has previously been identified by other authors (Klein et al. 2018). We conduct an extensive review of the literature to quantify in how far major crops are dependent on pollination services to produce seeds using dependence ratios, that indicate to what degree each crop depends on pollinators. We provide these ratios across major FAO crops and selected crops of economic relevance that are not included in the list of FAO crops. These particularly include forage crops like alfalfa and different species of clovers. While the economic relevance of animal mediated pollination services for seed production has been discussed for a long time (Winston and Scott-Dupree C. 1984; Southwick and Southwick 1992), it interestingly has been ignored by economic valuations of pollination services (Melathopoulos et al. 2015). Our investigation can therefore provide valuable information for economic assessments on the value of pollination services in seed production. Moreover, we discuss limitations of dependence ratios and provide insights for future research on the role of pollinators in seed production.

Materials and Methods

The starting point of this review was to identify which major crops might be dependent on pollinators to produce seed. To this end we started by analyzing the list of FAO crops, which is a comprehensive list of major global crops (FAO 2023).

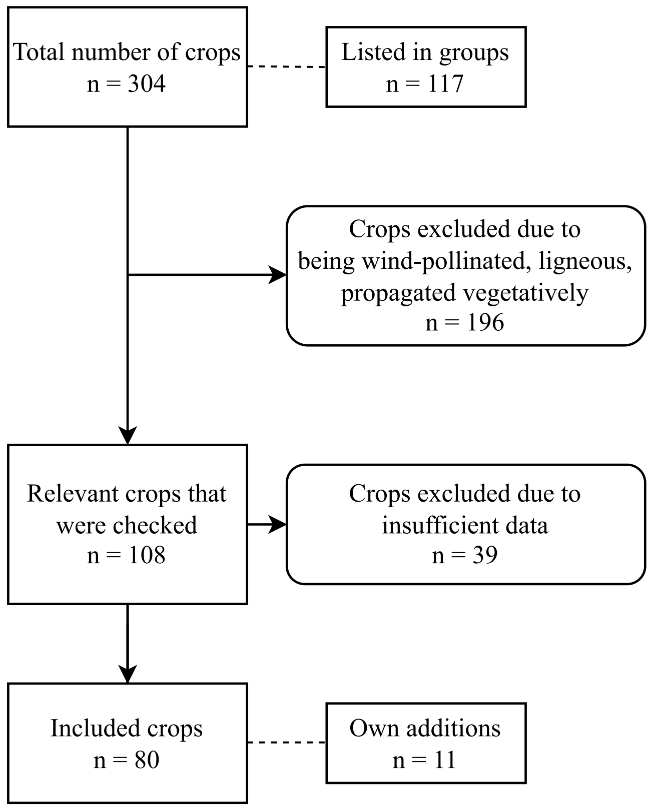

Figure 1 - Flowchart depicting crop selection process. 304 crop species were taken from the list of FAO crops, with 117 crop species being listed in groups. Out of these 304 crops, 196 crops were excluded because they are wind-pollinated (Klein et al. 2007), ligneous, or propagated vegetatively. Out of 108 crops, 39 crops had to be excluded due to insufficient information being available. Lastly, 69 FAO crops ended up in the final analysis with 11 foraging crops being added to the review, resulting in 80 analyzed crops.

The FAO crop list does not name scientific species, instead it names commodities. For example, it only lists the common name of a crop (e.g. tomatoes) in the FAO list, while for the literature review we would also need to search for the scientific name of the crop (e.g. *Lycopersicon esculentum* for tomatoes). Our matching between commodity and crop species is based on the work of previous authors (Klein et al. 2007). Our analysis of the FAO crop list starts with 304 crops (*Figure 1*), which also includes 117 crops that were listed in groups. Groups consist of multiple crops (e.g. a spices group consisting of anise, badian, coriander etc.), which were separated into individuals crop species. In the next step we removed 196 crops from the list, which are wind-pollinated, ligneous, or propagated vegetatively (*Figure 1*). Wind-pollinated crops, like the major cereals, do not depend on pollinators and are therefore removed (Klein et al. 2007). Ligneous crops, i.e. tree and shrubs, where removed as they can be propagated vegetatively through grafting or rootstock and do not rely on pollinators for propagation purposes. Moreover, we removed crops that are mostly vegetatively propagated like strawberries, as they also do not rely on pollinators to be propagated. Pollination services play an important role in the genetic recombination of such crops and in the creation of new varieties, but for this review the focus is on the primary production of seed and not on the creation of new varieties. We ended up with 108 crops that needed investigation.

After this initial screening, a literature review was conducted using the scientific database Scopus to identify relevant literature. The following general keywords were used to search the database: "polli*" & "scientific name" & "common English name". The full text of these papers was screened for information about the seed dependence ratio. The seed dependence ratio (SDR) expresses how much of a crop's seed yield is dependent on animal mediated pollination services. The SDR is thus calculated as follows:

$$SDR = 1 - \left(\frac{y_{wp}}{y_p}\right)$$

where y_{wp} represents the seed yield without pollinators present and y_p represents the yield with pollinators present. Note, that the general dependence ratio (DR), that expresses how much primary production depends on pollinators (Klein et al. 2007), is calculated the same way. We aimed to calculate the seed yield as the mass per area where possible. This metric was chosen, as it most closely represents the final product of seed production. Only including the number of seeds might ignore the fact that the seeds are significantly smaller than normally produced seeds, which might influence its viability for producers. As previous work has shown that pollination services affect seed weight and seed quality (Bommarco et al. 2012), we include at least one metric that reflects this effect. Some studies, however, only reported yields per fruit, yields per plant or tons per ha. Given this discrepancy, we aimed at calculating the closest metric, meaning that if possible we multiplied changes in fruit numbers with changes in seed numbers and if possible with changes in seed weight. This was unfortunately not always possible as not all yield components were reported across the identified studies. Studies that reported only the seed set where not included in our analysis as this does not provide sufficient information about the final seed yield. We therefore only included studies that reported absolute changes. Once we identified the dependence ratio of each crop we classified them following the same scheme proposed by Klein et al. (2007) as this allows for a good overview of the dependence across the analyzed crops. This scheme differentiates between five categories of dependence levels, which is determined whether a reported dependence ratios falls between the respective minimum and maximum range as reported in *Table 1*. Putting a crop in the category "no increase" for example, would indicate that the production of seed does not depend on pollinators at all, while the category "essential" indicates that a crop would lose most of its yield should there be no pollination available (*Table 1*). It should also be noted that for SDR that are 100%, we set the SDR to 99% as it eases future calculations and allows for a small error term across studies. This deliberate step was also undertaken, as economic analysis cannot work with a SDR of 100% (Lippert et al. 2021). After calculating the mean SDR of each identified study, we averaged the SDR for each respective crop, enabling us to classify each crop into one of our five categories (*Table 1*).

Table 1 - Scheme for categorization of dependence ratios following Klein et al. (2007)

		Dependence ratio		
		Mean	**Minimum**	**Maximum**
Dependence category	No increase	0	0	0
	Little	5%	>0%	<10%
	Modest	25%	>=10%	<40%
	High	65%	>=40%	<90%
	Essential	95%	>=90%	<=100%

Once we screened the literature, searching for the relevant information on SDR, we further excluded 39 crops from our analysis, as we did not find sufficient information for them (*Figure 1*). For 33 crops we were able to retrieve SDR from the study by Klein et al. (2007), as for some crops the SDR is equal to the DR (e.g. soybean). In the end, we analyzed the SDR of 36 FAO crops. In addition to the FAO crops we also included 11 major forage crops such as clovers and alfalfa as they have previously not been covered by any review. In addition, to the SDR, we also collected information on the study location and the experimental setup. The list of all analyzed crops can be found in Appendix A.

Results

For the review we ended up analyzing 110 different studies, which reported relevant information on SDR. Most studies were conducted in the USA, Brazil, India, Australia and New Zealand (*Figure 2*). Interestingly, except for the studies conducted in Mexico and Brazil, no studies from other countries in Latin America were found. Furthermore, Central and Southeastern Asia as well as most of the African continent is underrepresented in our reviewed studies.

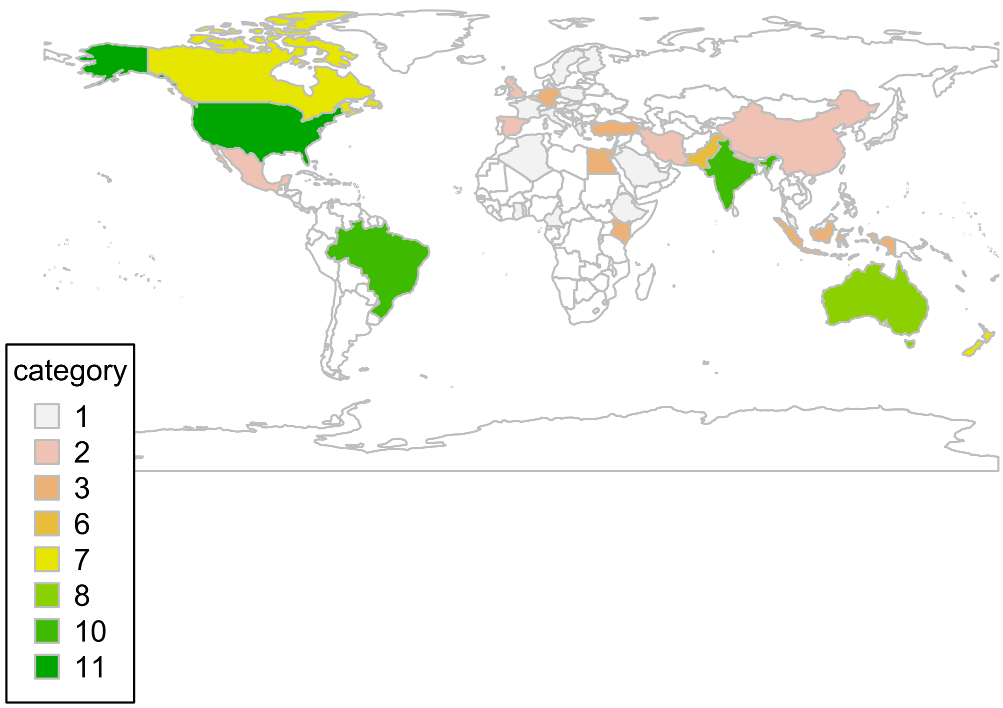

Figure 2 – Map showing the location and number of studies included in the review.

Based on the 110 identified studies, we were able to identify the SDR for 47 different crops. Using the classification scheme reported in Table 1 to structure the findings from the literature, we can see that 16 crops essentially depend on insect pollination, 19 have a high dependence, 2 crops that have a modest dependence, 3 crops that have a little dependence and 7 crops that do not depend on insect pollination (*Figure 3*). It can bee seen that out of the reviewed crops a large number of crops rely on pollinators to produce seeds. A list of all crops reviewed with their respective seed dependence ratio can be found in Appendix A.

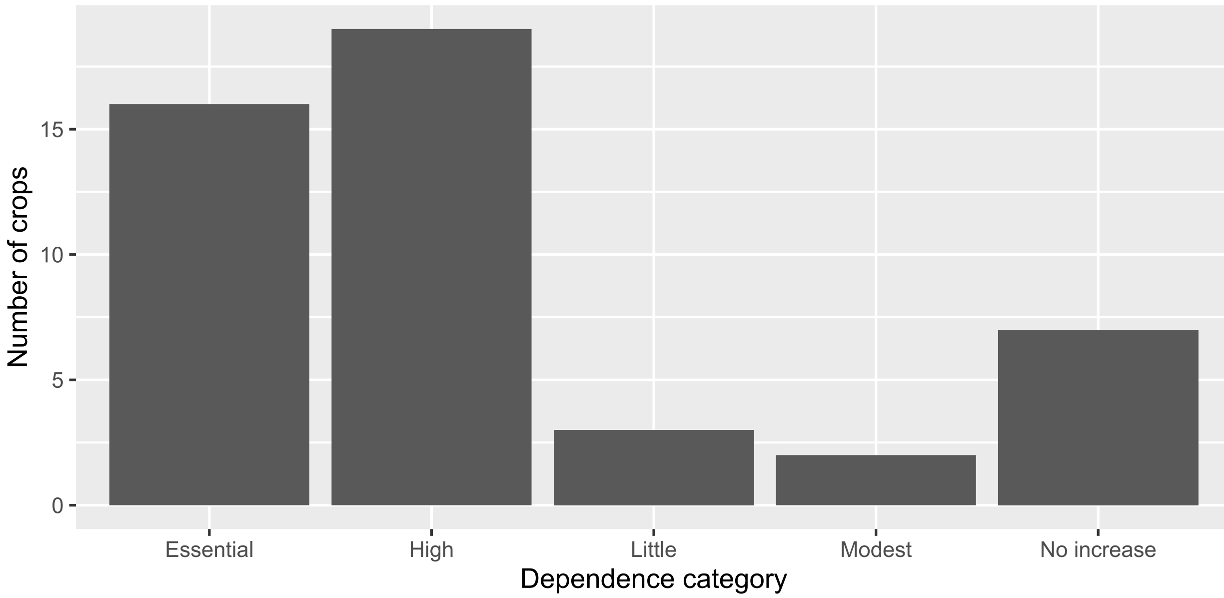

Figure 3 - Dependence categories following categories presented in Table 1. A list of all crops is available in Appendix A.

Analyzing the specific SDR we retrieved from the reviewed studies, we can observe great differences across the 47 reviewed crops (*Figure 4*). First, we can see that for some crops we were able to retrieve a good number of studies compared to other crops. For example, for tomato (*Solanum lycopersicum*) we identified 12 different studies, while for asparagus (*Asparagus officinalis)* we were only able to find one single study (*Figure 4*). Lastly, if we compare the SDR with the DR provided by Klein et al. (2007), we can observe that some crops, like asparagus or artichoke, do not depend on pollinators to produce fruits but they do indeed depend on pollinators to produce seed (*Figure 4*). Moreover, for various crops we can even observe a double dependence where both fruit and seed production do depend on pollinators (e.g. cucumber). This double dependence is especially high in the case of zucchini and watermelon, which both essentially depend on pollinators.

We also analyzed whether there is a difference between SDR, if they are retrieved from a study that was conducted in a greenhouse or in a field experiment. However, there were not enough studies available to make a statistically significant comparison and the mean of each study also does not indicate any general trend (*Figure 5*). Overall, it can at least be said that more studies were conducted inside a greenhouse and that especially for tomato more field experiments are needed (*Figure 5*).

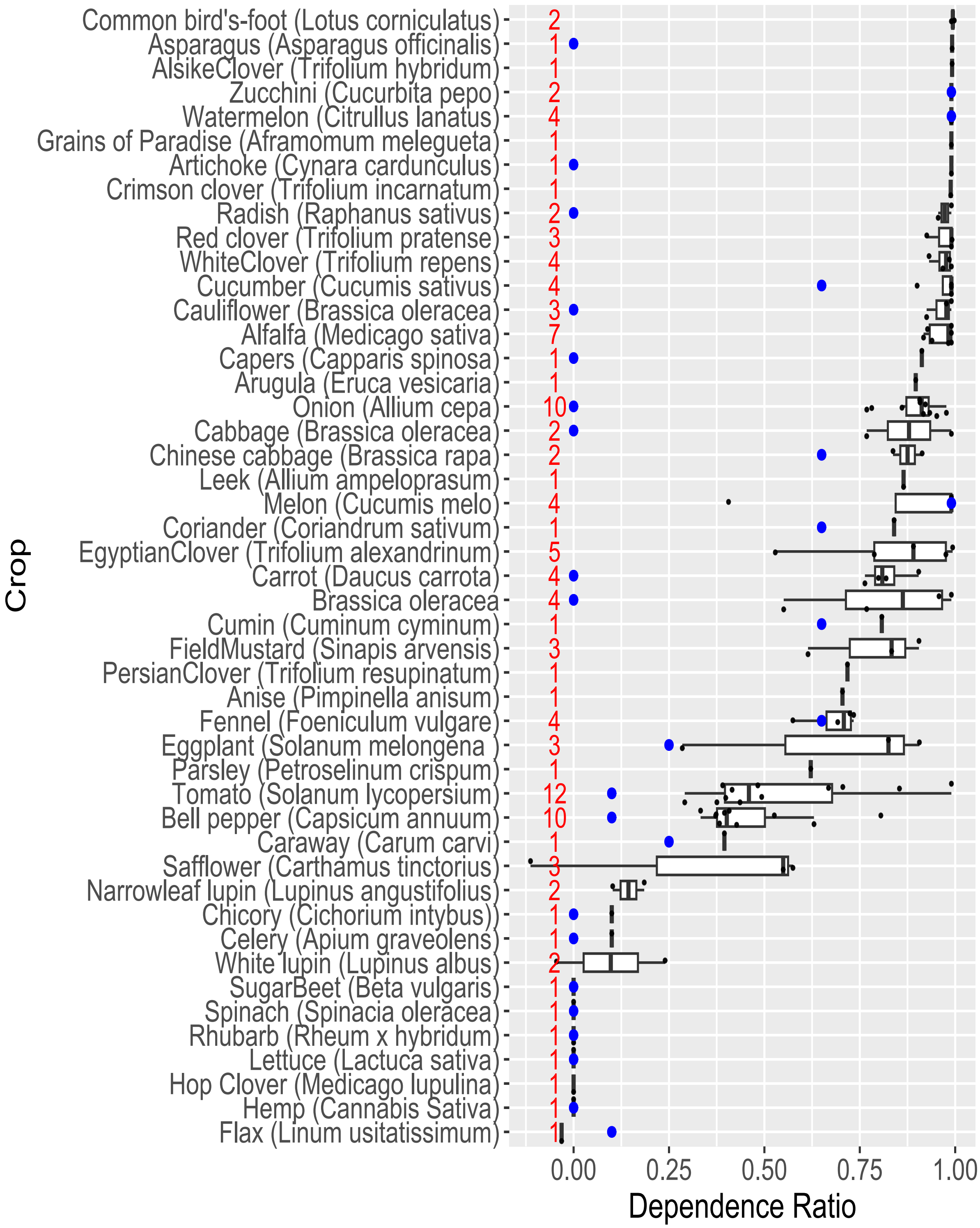

Figure 4 - Mean seed dependence ratio of each reviewed study for the 47 crops included in the review. The common name of the crop is reported in the first place followed by the respective scientific name. The numbers printed in red font report the number of studies reviewed for each crop. The blue datapoints represent the food or fruit dependence ratio (if available) as reported by Klein et al. (2007). The boxplots indicate the seed dependence of the respective crops and the black bars indicate the respective median of each reviewed study. The exact numerical mean of each crop is reported in Appendix A.

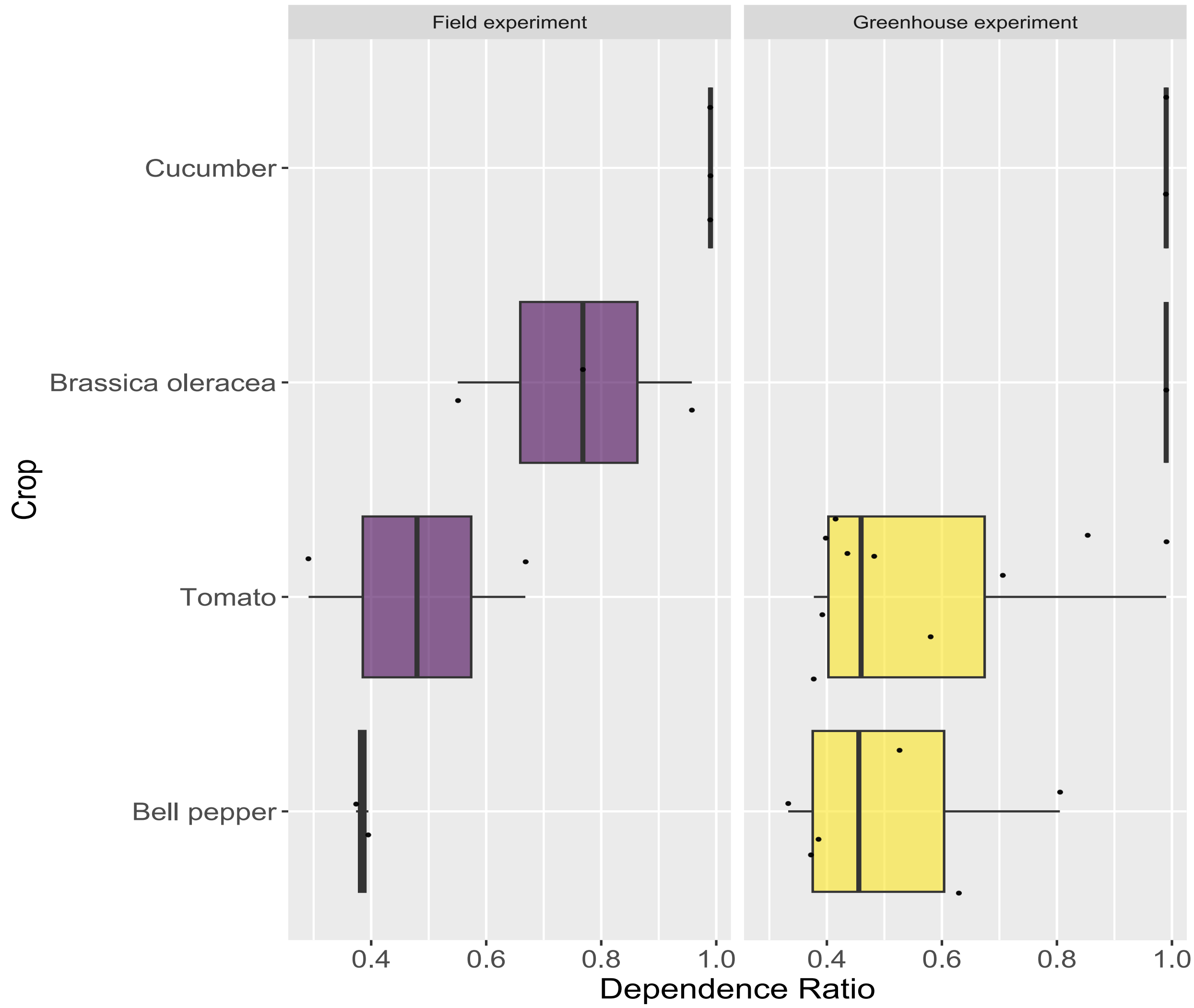

Figure 5 – Comparison of mean seed dependence ratio between field and greenhouse experiments. Black dots indicate the mean of each respective study that was used to plot the boxplots. Only crops where more than two studies for each treatment were available are shown here.

Discussion

The identified studies show that there is a high number of crops that depend on animal-mediated pollination to produce seed. Focusing only on the DR, therefore, underestimates the relevance of pollinators in agricultural systems. This is an important insight as DR have been widely used in economic valuation studies (Gallai et al. 2009; Lippert et al. 2021), which could potentially be extended using the reviewed SDR. Moreover, pollination services are increasingly represented in national accounts (Alexandris et al. 2018) and it could therefore also be of interest to include SDR to national ecosystem service accounting, especially for large seed producing countries (e.g. the Netherlands, France or the USA). Given that we followed the same categorization as Klein et al.

(2007) our SDR can be easily included in already existing ecosystem service models, like inVEST (Sharp et al. 2014), which have recently been linked to economic models (Johnson et al. 2023). This would allow for sophisticated analysis of the role of seed production in ecological-economic systems.

We also want to highlight that the SDR allows for more complex analysis of the role of pollination services across the agricultural production chain. This is especially important for crops where a double dependency on pollinators, like cucumbers, exists. This double dependency could potentially prove to be a significant risk for smallholder farmers who often produce a significant amount of their own seeds (McGuire and Sperling 2016). Future research could therefore investigate how a change in pollination services across multiple seasons could affect both seed and food production of smallholder farmers and what this potentially implies for food security. Considering that this double dependency exists mostly for vegetables, that are linked to nutritious diets, it would also be of interest to see how this is related to the dimension of health (Smith et al. 2022).

SDR and DR are based on studies that use insect exclusion experiments, which often simulate the total extinction of all pollinators. This is a rather extreme scenario and further investigation should explore how marginal changes affect the seed production of crops. These marginal changes, that have only been explored for a few crops like coffee (Ricketts and Lonsdorf 2013), are interesting for seed producers in particular, as they can be directly linked to the decision making process of the seed producer. Moreover, knowing how seed yield responds to marginal changes in pollination services, would make it possible to identify threshold values, at which a change in pollinator numbers could have substantial effects on the yield of a given crop (Hanley et al. 2015). Given the relatively large number of crops that were identified in this study, which rely on pollinators to produce seeds, it would most likely require substantial effort to investigate these marginal changes. Moreover, these values are not only missing for the SDR but also for most DR. It might therefore be sensible to focus on major crops first. Lastly, it should also be highlighted that pollination services affect the yield in complex ways beyond the simple quantity produced, as these services also affect the quality of a given crop (Wietzke et al. 2018). The SDR calculated in this study therefore ignore important aspects of pollination services and should be extended once more detailed data is available. Reflecting on the SDR and DR it should also be mentioned that there is no standardized experiment for conducting pollination exclusion experiments, which to some degree limits the comparability of the SDR across studies. This nevertheless should not limit the general trends indicated in our study, especially for crops that essentially depend on pollination to form seeds. The values of dependence ratios presented here might be even higher in hybrid breeding systems, as male sterility makes a plant less attractive to pollinators (Gaffney et al. 2019). This fact has already gained the attention of the scientific community and research, with the aim of increasing the attractiveness of hybrid breeding crops to pollinators, is already being conducted (Gaffney et al. 2020). As the number of hybrid varieties on the market is increasing (Santamaria and Signore 2021), genetic traits that make crops more attractive to more pollinators should gain in importance. For some crops like Egyptian clover the reported studies showed great variance across different varieties showing that for some crops the dependence on pollinator could potentially be reduced (Beri et al. 1985), while for other crops that essentially depend on pollinators this might not be possible.

Reflecting on the role of pollinators in seed production, it needs to be mentioned that declining pollinators could be either substituted through manual labor (Wurz et al. 2021) or even new technologies such as drones (Hiraguri et al. 2023). This holds true especially for crops propagated in greenhouses but might not be as relevant for crops propagated outside like alfalfa which have more complicated pollination mechanisms. In our review, we did not analyze which pollinators are the most relevant pollinating species for a respective crop, but it would be very interesting to analyze which pollinators can be substituted by others and in how far pollination services could be completely substituted through hand pollination. Here we only focus on one service that pollinators potentially can provide but there are of course others that have not been mentioned, like pest control (Pekas et al. 2020) or reduction of pollen exposure of greenhouse workers (Jong et al. 2006).

We also want to highlight that focusing only on FAO crops ignores many important crops that also rely on pollination services, like the forage crops covered in this review, but also of other less researched crops in developing countries, where a greater variety of crop species still exists. Given the linkage of crop diversity and food security, future research needs to also focus on crops that are not listed in the FAO crop list, which locally might be highly important (Makate et al. 2016).

Given the limited amount of studies identified through Scopus it seems that research on seed yield and pollination is still lacking, which has also been reported by other authors (Jing et al. 2021). This makes more sophisticated statistical analysis like meta-regression very difficult and is also the main reason while we followed the simple approach of SDR and DR. It is therefore crucial to further research the role of pollinators in seed production through field experiments and integrate this information in already existing databases, which can be an important next step to supplement the already existing knowledge (Balfour et al. 2022).

Conclusion

This study emphasizes the critical importance of pollination services in seed production for a wide range of crops. The findings reveal that numerous crops, including most vegetable and forage crops, rely on insect pollinators to produce seeds, which also serve as the foundation for agricultural supply chains. Understanding the variations in dependence ratios is vital for assessing the potential risks associated with changing pollinator populations. The study sheds light on the underestimated double dependence of certain crops, where both fruit and seed production rely on pollinators. This has significant implications for smallholder farmers who save and replant their seeds. The research calls for greater consideration of pollination services in economic assessments and databases, as well as a deeper exploration of marginal changes in pollinator populations and their impact on seed production. Additionally, the potential for technology and alternative pollination methods, especially in greenhouse settings, deserves further examination. Overall, this study emphasizes the multifaceted importance of pollinators in global agriculture and the need for their conservation. It contributes to our understanding of the intricate relationship between pollinators, seed production, and food security, highlighting the urgency of protecting and preserving these essential contributors to our food supply.

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Appendix A

Crop name	**Seed dependence ratio**	**Categories**	**Dependence ratio** (Based on Klein et al. 2007**)**	**Double dependence**
Alfalfa (Medicago sativa)	0.962	Essential	"n.a."	
Alsike Clover (Trifolium hybridum)	0.992	Essential	"n.a."	
Anise (Pimpinella anisum)	0.705	High	"unknown"	
Artichoke (Cynara cardunculus)	0.99	Essential	0	
Arugula (Eruca vesicaria)	0.897	Essential	"n.a."	
Asparagus (Asparagus officinalis)	0.992	Essential	0	
Bell pepper (Capsicum annuum)	0.475	High	0.1	X
Brassica oleracea	0.817	High	0	
Cabbage (Brassica oleracea)	0.879	High	0	
Capers (Capparis spinosa)	0.913	Essential	0	
Caraway (Carum carvi)	0.395	High	0.25	X
Carrot (Daucus carrota)	0.821	High	0	
Cauliflower (Brassica oleracea)	0.964	Essential	0	
Celery (Apium graveolens)	0.1	Little	0	
Chicory (Cichorium intybus))	0.1	Little	0	
Chinese cabbage (Brassica rapa)	0.879	High	0.65	X
Common bird's-foot (Lotus corniculatus)	0.994	Essential	"n.a."	
Coriander (Coriandrum sativum)	0.84	High	0.65	X
Crimson clover (Trifolium incarnatum)	0.988	Essential	"n.a."	
Cucumber (Cucumis sativus)	0.99	Essential	0.65	X
Cumin (Cuminum cyminum)	0.808	High	0.65	X
Eggplant (Solanum melongena)	0.672	High	0.25	X
Egyptian Clover (Trifolium alexandrinum)	0.835	High	"n.a."	
Fennel (Foeniculum vulgare)	0.681	High	0.65	X
Field Mustard (Sinapis arvensis)	0.784	High	"n.a."	
Flax (Linum usitatissimum)	-0.031	No increase	0.1	X
Grains of Paradise (Aframomum melegueta)	0.99	Essential	"unknown"	
Hemp (Cannabis Sativa)	0	No increase	0	
Hop Clover (Medicago lupulina)	0	No increase	"n.a."	
Leek (Allium ampeloprasum)	0.865	High	"n.a."	
Lettuce (Lactuca sativa)	0	No increase	0	
Melon (Cucumis melo)	0.844	High	0.99	X
Narrowleaf lupin (Lupinus angustifolius)	0.144	Modest	"n.a."	
Onion (Allium cepa)	0.893	High	0	
Parsley (Petroselinum crispum)	0.621	High	n.a.	
Persian Clover (Trifolium resupinatum)	0.718	High	"n.a."	
Radish (Raphanus sativus)	0.973	Essential	0	
Red clover (Trifolium pratense)	0.969	Essential	"n.a."	
Rhubarb (Rheum x hybridum)	0	No increase	0	
Safflower (Carthamus tinctorius)	0.337	Modest	n.a.	
Spinach (Spinacia oleracea)	0	No increase	0	
Sugar Beet (Beta vulgaris)	0	No increase	0	
Tomato (Solanum lycopersium)	0.547	High	0.1	X
Watermelon (Citrullus lanatus)	0.99	Essential	0.99	X
White lupin (Lupinus albus)	0.097	Little	"n.a."	
White Clover (Trifolium repens)	0.968	Essential	"n.a."	
Zucchini (Cucurbita pepo)	0.99	Essential	0.99	X