ELSEVIER

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee





The vital role of pollination services in seed production: A global review

Falk Krumbe * 0, Simone Melder 0, Arndt Feuerbacher 0

Ecological and Economic Policy Modelling Research Group, University of Hohenheim, Schwerzstr. 46, Stuttgart 70599, Germany

ARTICLE INFO

Keywords:
Biodiversity
Crop productivity
Ecosystem services
Pollinator declines

ABSTRACT

Animal pollinators play a fundamental role in the reproductive processes of both wild and cultivated plants, impacting global agriculture. In the face of global declines in biodiversity, especially in insect biodiversity, this study reviews the critical role of pollination services in the seed production of food crops. While previous reviews assess the influence of pollinators on primary food production, this review extends it 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 of major crops that are propagated via seeds. Out of the 74 crops analyzed, 17 depend essentially on pollinators, 22 are highly dependent, 8 moderately dependent, whereas 1 shows little dependence and 6 no dependence at all. For 20 crops no conclusive data has been found. Globally significant crops, such as carrots and various clover species, are among the identified pollinator-dependent species. Moreover, some of the crops do not rely on pollinators for primary production, and are thus potentially overlooked in assessments that focus solely on fruit yields. Lastly, we highlight the importance of analyzing the effect that pollinators have on different yield components, the economic value of pollinators in seed production, and the need for further research on the contribution of pollinators to seed production.

1. Introduction

The dramatic decline in biodiversity (Hallmann et al., 2017; Seibold et al., 2019) threatens the functioning of ecosystems and the provision of vital ecosystem services (Dangles and Casas, 2019). Animal pollinators, such as insects (Rader et al., 2016), bats (Ramirez-Francel et al., 2022), or birds (Regan et al., 2015), play a key role in the reproduction of both wild (Rodger et al., 2021) and cultivated plants (Klein et al., 2007; Siopa et al., 2024). The potential consequences of changing pollinator numbers on crop production have been analyzed by various studies, investigating, for example, effects on yields (Schurr et al., 2022), protein content (Fijen et al., 2021), crop quality (Gudowska et al., 2024) or yield stability (Hünicken et al., 2021). Klein et al. (2007) and Siopa et al. (2024) provide an overview of the dependence of crops on pollinators. Their studies focus on the primary production of agricultural produce, that means, the production of plant parts for direct or indirect human consumption. The role of pollinators in other production systems, like seed production, is not directly covered by their analyses. For instance, the carrot (Daucus carota L.) does not rely on pollinators to produce its taproot (Klein et al., 2007). However, its flowers may depend on pollinators to produce the seed needed for crop propagation. With our research, we aim to fill the gap that has previously been identified (Klein et al., 2018). We conducted an extensive literature review to quantify the extent to which globally important crops rely on pollination services for seed production. We report these dependencies across major FAO crops and other selected crops of economic relevance, particularly forage crops like alfalfa (Medicago sativa L.) and different species of clovers. These dependence assessments are especially useful for economic valuation studies that have highlighted the role of pollinators in securing economic welfare (Lippert et al., 2021) and food security (Smith et al., 2015; Feuerbacher, 2025), but have so far ignored the role of pollinators in seed production apart from one study (Feuerbacher et al., 2024). Our investigation can therefore provide valuable information for economic assessments on the value of pollination services in seed production. We further highlight how the inclusion of different yield components can influence the degree of dependence on pollination services. Lastly, we discuss the limitations of seed dependence ratios (SDRs), which measure the extent to which a crop's seed production depends on animal-mediated pollination services, and provide insights for future research on the role of pollinators in seed production.

E-mail address: falk.krumbe@uni-hohenheim.de (F. Krumbe).

 $^{^{\}star}$ Corresponding author.

¹ Klein et al. (2007) already provide an indication which crops rely on pollinators for seed production but no numeric values or dependence categorization.

2. Materials and methods

The starting point of this review was to identify which major crops are dependent on pollinators to produce seed. To this end, the list of FAO crops, which is a comprehensive list of major global crops (FAO, 2023), was analyzed. The FAO crop list does not name scientific species, instead it names food crop commodities. Our matching of commodities to their corresponding crop species is based on the work of previous authors (Klein et al., 2007) and is documented in Supplementary Material A. Some crops are listed in groups that contain multiple species (e.g., a spices group consisting of anise (*Pimpinella anisum* L.), coriander (*Coriandrum sativum* L.), etc.), that are separated into individual crop species. In the beginning, a total of 283 crops were identified, with 117 coming from listings in groups.

In the next step, 184 crops were removed from the list, as they are either wind-pollinated, ligneous, or reproduce vegetatively. Windpollinated crops, such as the major cereals, do not depend on pollinators and were therefore excluded (Klein et al., 2007). Ligneous crops, including trees and shrubs, were removed because the vast majority can be reproduced asexually through grafting or rootstocks and do not rely on pollinators for reproduction. Additionally, we eliminated other crops that primarily reproduce asexually, like strawberries, as they also do not depend on pollinators for this process (Debnath, 2013). Pollination services play an important role in the genetic recombination of such crops and in the creation of new varieties (Klein et al., 2007), but for this review, the focus lies on the primary production of seed and not on the creation of new varieties. Next, 37 crops that have identical seed and fruit yield (e.g., beans) were removed, as they have already been covered in the publication by Klein et al. (2007). In the end, 62 crops were identified for the review, which will be described shortly. The FAO list of crops excludes fodder crops such as clover and other horticultural crops of interest, so we supplemented it by adding 12 relevant crops, bringing the total to 74 analyzed crops. The list of added crops can be found in Supplementary Material A.

For 20 of the analyzed crops, we did not find any scientific studies and for seven we did not find numeric values but rather an indication of their dependence (e.g., no dependence on pollinators for spinach (*Spinacia oleracea* L.)). Lastly, for 47 crops we were able to extract exact SDRs (Fig. 1).

After the initial screening, a literature review was conducted using the scientific database Scopus. The following general keywords were used to search the database: "polli*" & "scientific name" & "common English name". The database search was finalized on April 1, 2024. A total of 8057 abstracts and titles were screened (6131 without duplicates), resulting in 116 full-text articles being included in the final analysis. While the majority of articles were sourced from Scopus, a few additional relevant studies were manually included. The full list of all screened abstracts and titles is available upon request. Articles were included in the final analysis if they either compared seed numbers with and without pollinators or indicated that no fruits form in the absence of pollinators, preventing seed development in crops where seeds form within fruits. Studies that report only the seed set were not included in our analysis as this does not provide sufficient information about the final seed yield. Further, we included studies conducted in both

greenhouses and in the field. Exclusion of pollinators was accomplished by covering the flowers with bags, caging the entire plant, or preventing all pollinators from accessing the greenhouse. In addition to data on seed numbers with and without pollinators, information on the number of fruits, seed weight, and germinability of the respective crops was collected when available. The analysis aimed to compare seed yield under open pollination (i.e., unrestricted field conditions) and closed pollination. However, in some studies, only supplementary pollination data (e.g., from greenhouse studies) were available, which were used in those cases. Data were extracted from tables, supplementary materials and plots using WebPlotDigitizer (Rohatgi, 2024). Lastly, it is important to note that many of the analyzed studies did not focus primarily on comparing the effects of animal-mediated pollination services on crop seed yield; instead, they addressed other topics, with seed yield reported as a supplementary statistic.

The collected values were then used to calculate the SDR, i.e., how much seed production of a respective crop depends on animal-mediated pollination services. It is analogous to the dependence ratio (DR) used in other studies (Klein et al., 2007; Siopa et al., 2024), which focuses on primary production (e.g., fruit production of a crop), whereas the SDR is focused on seed production. The SDR is calculated as follows:

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

where y_{wp} represents the seed yield without pollinators present and y_p represents the yield with pollinators present. The subscripts p and p indicate the yield with and without pollinators. Note that the DR is calculated in a similar manner (Klein et al., 2007). We aimed to calculate the SDR using mass per unit area or mass per plant whenever possible, as this metric most accurately reflects the final product of seed production, making it particularly relevant to seed producers. In cases where seed yield was reported as mass per unit area or mass per plant, equation (1) is sufficient to calculate the SDR. However, focusing only on crops and studies reporting yield as mass per unit area or mass per plant, would significantly restrict the scope of the study. We therefore aimed to calculate these values as close as possible, using other yield components. Therefore, if available, the yield was calculated as follows:

$$\frac{y_{wp}}{y_p} = \frac{s_{wp}}{s_p} \times \frac{f_{wp}}{f_p} \times \frac{sw_{wp}}{sw_p}$$
 (2)

where s_p and s_{wp} are the seed numbers with pollinators and without pollinators, respectively. Similarly, f_p , f_{wp} , s_{wp} and s_{ww} indicate fruit number and seed weight including and excluding pollinators. Most studies did not report all of these factors. To address this discrepancy, we aimed to calculate the most accurate value possible. This involved multiplying changes in fruit numbers with changes in seed numbers, and, when applicable, with changes in seed weight. In cases where seed weight (s_w) or fruit number (f) are not available, we set their value to 1. Equation (2) also lets us analyze the effect of different yield components on the final SDR. The SDR was then calculated by averaging each observed SDR per study and then averaging the SDR across all available studies to calculate the final SDR per crop.

Once the SDR of each crop had been calculated, 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. Said scheme differentiates between five categories of dependence levels, which determine whether a SDR falls between the respective minimum

² Some tree crops such as coconuts (*Cocos nucifera* L.) do rely on seed for commercial propagation but are not covered in this review, as their seed dependence ratio is equal to the dependence ratio, which has been reported by other reviews (e.g., Klein et al. 2007). In some cases, seeds are used for seedling production to function as a rootstock base, but given their limited importance, we did not include these cases in the review.

³ To our knowledge, the publication by Klein et al. (2007) was the most comprehensive review on dependence ratios at the time of writing. Recent publications offer a more detailed look at the dependence ratios of certain crops e.g., Franceschinelli et al. (2022).

⁴ We attempted to collect data on seed germinability; however, such information was available only in a few cases. Additionally, germinability is likely influenced by seed weight, which could result in redundant inclusion of the same effect. To ensure consistency, we focused our analysis on three primary yield components: seed number, fruit number, and seed weight. The impact of pollination on germinability is reported in Supplementary Material D.

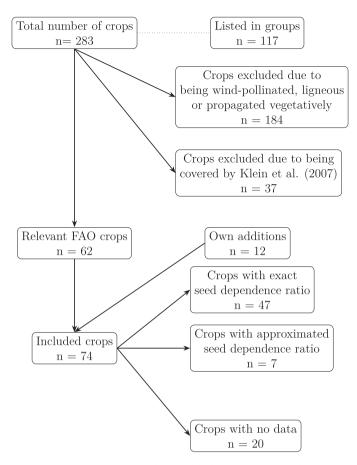


Fig. 1. Flowchart depicting crop selection process. 283 crop species were taken from the list of FAO crops, with 117 crop species being listed in groups. Out of these 283 crops, 184 crops were excluded, because they are wind-pollinated (Klein et al. 2007), ligneous, or propagated vegetatively. 37 crops were excluded, whose seed yield is equal to its fruit yield (e.g., beans) (Klein et al. 2007). The FAO list of crops excludes fodder crops such as clover and other horticultural crops of interest, so we supplemented it by adding 12 relevant crops, bringing the total to 74 analyzed crops. For 20 analyzed crops we did not find any scientific studies and for seven we were only able to approximate the seed dependence ratio based on other reviews (e.g., Klein et al. 2007). Lastly, for 47 crops the exact seed dependence ratio was extracted. Source: Authors' design.

Table 1 Seed dependence ratio categories.

Seed Dependence Category	Mean	Minimum	Maximum
No reduction	0	0	0
Little	0.05	>0	< 0.1
Modest	0.25	≥ 0.1	< 0.4
High	0.65	≥ 0.4	< 0.9
Essential	0.95	≥ 0.9	≤ 1

Note: Categories adopted from Klein et al. (2007).

and maximum range as reported in Table 1. Putting a crop in the category "no reduction", for example, indicates that the production of seeds does not depend on pollinators at all, while the category "essential" indicates that a crop would lose most of its yield, should no pollinators be present (Table 1). It should be noted that SDRs of 1 are sometimes expressed as 0.99, as it eases calculations. This is often done in economic studies, as economic analyses have difficulties working with a DR of 1 (Feuerbacher, 2025). In this publication, we did not alter any SDR to 0.99. A small subsection of seven crops was categorized without any direct experimental findings. These crops have been labeled as non-dependent on insect-pollination, like sugar beet (Beta vulgaris L.) or lettuce (Lactuca sativa L.) for example, throughout the reviewed literature and previous analyses (Klein et al., 2007). Among these seven crops, celery (Apium graveolens L.) and chicory (Cichorium intybus L.) were assigned a seed dependence ratio of 0.1, as the degree of dependence could not be quantified exactly. These crops are listed in Supplementary

Material B.

The SDRs calculated from certain studies on crops such as white lupin (*Lupinus albus* L.), sesame (*Sesamum indicum* L.), safflower (*Carthamus tinctorius* L.), and flax (*Linum usitatissimum* L.) yielded negative values. To the best of our understanding, this outcome is either attributed to the study design (e.g., the use of cages that inhibit growth) or an autogamy mechanism benefiting the number of seeds produced. In these cases we have chosen to set their SDR equal to 0, as the SDR indicates its reliance on pollinators which logically cannot be negative. In this context it is important to note that in our study we only focus on the seed output, but pollinators also aid the genetic recombination, which is not covered in this analysis.

To estimate the role of animal-mediated pollination in global seed production, we utilized data from the International Seed Federation (ISF, 2022), which provides export estimates for seed tonnage and value across countries, though it does not include crop-specific details. Therefore, we relied on the mean SDR across all crops. While broad, this approach underscores the impact of pollinators on the global seed production value chain. Our analysis focuses on vegetable crops, which are highly reliant on pollination services for both seed and fruit production. All calculations and graphs were performed using R Statistical Software (R Core Team, 2023), while the crop selection flowchart was generated with TikZ/PGF (Tantau, 2023). The utilized packages are documented in Supplementary Material E.

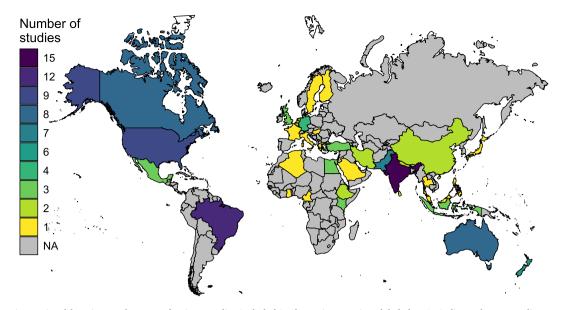


Fig. 2. Map showing national locations and counts of unique studies included in the review. Regions labeled "NA" indicate that no studies were found. Source: Authors' calculations.

3. Results

For the review we analyzed 116 different studies, which reported relevant information on SDRs. Most studies were conducted in India, Brazil and the USA (Fig. 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, the Iberian Peninsula, Eastern Europe as well as most of the African continent are underrepresented in the reviewed studies. ⁵

Based on the 116 identified studies, we calculated the SDRs for 47 different crops. For an additional seven crops no exact quantities were identified in the literature, but they have been labeled previously as wind-pollinated or slightly dependent and were thus included in this qualitative categorization. Using the classification scheme reported in Table 1 to structure the findings from the literature, we can see that 17 crops essentially depend on animal pollinators to produce seeds, 22 are highly dependent, eight crops are modestly dependent, one crop is little dependent and six crops do not depend on animal pollinators. Consequently, a substantial proportion of the crops examined depend on pollinators for seed production. For 20 crops, no data was found. A list of all crops reviewed with their respective SDR can be found in Supplementary Material B. Analyzing the specific SDRs we retrieved from the reviewed studies, we observe great differences across the 47 reviewed crops (Fig. 3). First, it is evident that a substantial number of studies exist for some crops, while others have been scarcely researched. For example, 12 studies were identified for tomato (Solanum lycopersicum L.), while only one study investigated asparagus (Asparagus officinalis L.) (Fig. 3).

Comparing the impact of including additional yield parameters (seed number, fruit number and seed weight) on the SDR reveals that the seed dependence ratio increases when changes in fruit numbers are incorporated (Fig. 4). Metrics of only seed numbers can therefore be misleading. In most cases, the inclusion of seed weight did not substantially affect the results. For crops, that form no fruit without

pollinators, like cucumber (Cucumis sativus L.), the SDR logically remains similar.

Calculating the average seed dependence ratio across all 54 crops yielded an average SDR of 0.63, which was subsequently multiplied by the seed export values. Analyzing the estimated contribution of pollinators to global vegetable production, it can be observed that a small number of countries, mainly the Netherlands, France, and the USA, benefit significantly from animal-mediated pollination services (Fig. 5). The total global contribution of pollinators to vegetable exports is estimated to be 2.987 billion USD in 2020.

4. Discussion

This study shows that animal-mediated pollination plays a significant role in the seed production of numerous crops. These crops include vegetable crops like tomato, cucumber, and zucchini (Cucurbita pepo L.) as well as important fodder crops like alfalfa and clover species. Pollination services are therefore not only of high relevance to the primary production of crops (Siopa et al., 2024) but also to the early steps of the production chain (i.e. seed production). Moreover, their relevance extends to other areas of agricultural systems that are usually not directly associated with pollination services, like animal production systems. Our analysis revealed considerable variation in SDRs across studies, suggesting that experimental setups substantially influence the calculations. Consequently, SDRs should be interpreted and applied with caution, taking the experimental context into account. In addition, the comparison of using SDRs based on different metrics revealed that the inclusion of more relevant yield factors can strongly influence the level of pollinator-dependence of a given crop. This holds true for most crops that do not essentially depend on pollinators. Crops that would not produce any fruit without pollinators, like cucumber or zucchini, are not subject to such implications.

Considering the trend of declining pollinator numbers (Dicks et al., 2021), this study's findings show that seed-producing companies and farmers are at risk, should these trends continue. Besides mitigation measures, like reverting negative pollinator population trends, there are an increasing number of studies analyzing potential substitutes for natural pollination services such as manual pollination (Wurz et al., 2021) or even new technologies such as drones (Hiraguri et al., 2023). These adaptation measures have not yet been explored thoroughly. The scope and whereabouts of potential applications remain unclear since

⁵ Considering these discrepancies, we ran additional queries on Scopus for a select number of crops (tomato, cucumber, zucchini, alfalfa, watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), melon (*Cucumis melo* L.), coriander, naranjillo (*Solanum quitoense* Lam.)), using Spanish keywords. The aim was to avoid potential language biases for important research regions like Argentina or Spain. These queries did not result in any new studies being identified.

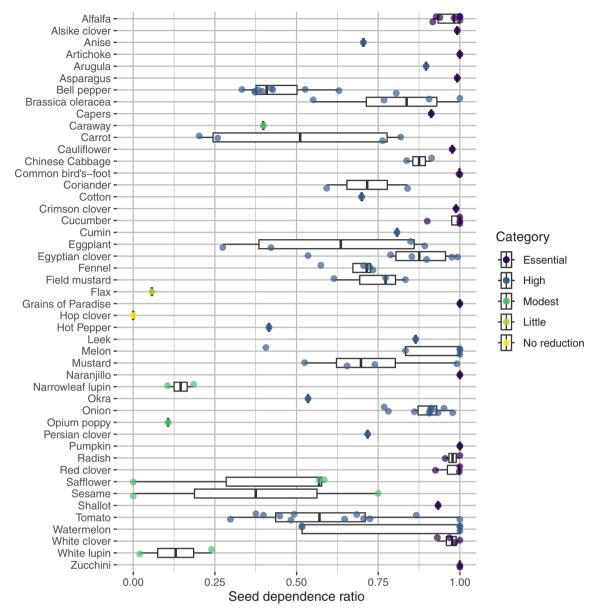


Fig. 3. Mean seed dependence ratios for each reviewed study across the 47 crops are presented. The boxplots illustrate the distribution of seed dependence ratios calculated across the identified studies. Each point indicates the mean seed dependence ratio of a given study. The precise numerical means for each crop per study can be found in Supplementary Material C. Crops are color-coded according to the categories outlined in Table 1. Source: Authors' calculations.

artificial pollination is most likely easier for crops with relatively simple pollination mechanisms, where mechanical solutions already exist (e.g., tomatoes) (Cooley and Vallejo-Marin, 2021), compared to field crops with relatively complicated pollination mechanisms like alfalfa. Lastly, these adaptation measures potentially ignore other benefits of pollinators, like pest control (Pekas et al., 2020), potential health benefits from reducing the pollen exposure of greenhouse workers (de Jong et al., 2006), and the importance of pollinators for non-commercial flowering plants (Rodger et al., 2021).

Smallholder farmers who produce their seed on their own (McGuire and Sperling, 2016) are particularly at risk if they are growing pollinator-dependent crops for seed and fruit production (e.g., cucumbers) (Cely-Santos and Lu, 2019). A substantial decline in pollinators would affect farmers not only in a given season but also in following seasons, as they would have fewer seeds available for continued crop production. In addition, vegetables, essential for adequate nutrition, are particularly dependent on pollinators for both seed and fruit production, thereby strengthening the link between pollination services and food

security (Smith et al., 2015). One aspect related to smallholder farmers that we did not address in our study is the fact that smallholder farmers grow crops from seeds even when asexual propagation is possible, such as using cassava seeds instead of stem cuttings.

The dependence ratios provided by Klein et al. (2007) have been widely employed in economic studies assessing the monetary value of pollination services (Gallai et al., 2009; Lippert et al., 2021). These assessments could now be extended using the SDRs presented in this study, highlighting the economic importance of pollinators. A recent publication has done this with values based on a previous working paper version (Feuerbacher et al., 2024). Pollination services are also increasingly represented in national accounts (Vallecillo et al., 2018) but to our knowledge, they only capture value in primary production and not seed production. Countries like the Netherlands, France, and the USA could therefore benefit from also including seed pollination services in their national accounts. Data on country-specific vegetable seed production in both tonnage and value would make a more sophisticated and detailed analysis of the role of pollinators in seed production

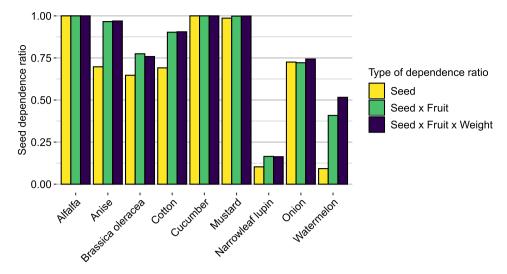


Fig. 4. Comparison of different seed dependence ratios for seed production, including only the change in seed number, the change in seed number and fruit number, and the seed number, fruit number and seed weight. Crops were only included if information on seeds, fruits and seed weight were available. Studies with negative seed dependence ratios were not included. Authors' calculations.

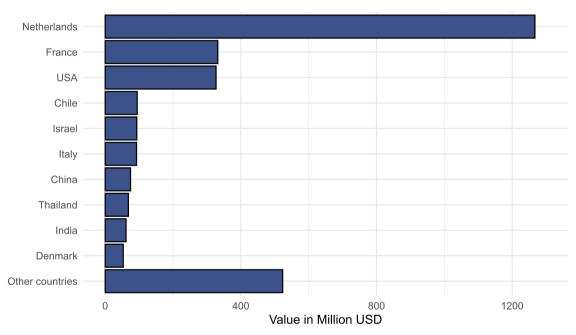


Fig. 5. Contribution of pollinators to global vegetable seed exports. Export data from 2020 statistic, by the International Seed Federation (ISF, 2022). Source: Authors' calculation.

possible and enable a direct link to national accounts.

Given that we followed the same categorization as Klein et al. (2007), our new SDRs can be easily included in already existing ecosystem service models like InVEST (Natural Capital Project, 2025), which are increasingly linked to economic models (Banerjee et al., 2022; Johnson et al., 2023). This would allow for sophisticated analyses of the role of seed production in ecological-economic systems and enable direct analysis of the link between agri-environmental policies, agricultural production, pollinator populations, and pollination services (Image et al., 2022).

The SDRs derived in this study as well as in previous research (Klein et al., 2007; Siopa et al., 2024), are based on pollinator exclusion experiments that compare crop yields with and without direct pollinator access. This scenario is quite extreme, underscoring the necessity for further investigation into how marginal changes in pollinator presence

may affect the SDRs of various crops. These marginal changes, which have been studied for only a limited number of crops (Ricketts and Lonsdorf, 2013), are particularly relevant to seed producers, as they can be directly linked to decision-making processes. Further research could therefore investigate how far these marginal changes affect important yield parameters of crops in both seed and fruit production, but also other aspects like crop quality (Wietzke et al., 2018). Some crops, like Egyptian clover (*Trifolium alexandrinum* L.) or blueberry (*Vaccinium* L.), show variance in dependence on pollinators across different varieties, which is an important factor that should also be considered in future investigations (Beri et al., 1985; Eeraerts et al., 2024). The SDRs identified in this study might be even higher in hybrid breeding systems, as male sterility, an important biological characteristic used in plant breeding, makes plants less attractive to pollinators (Fijen et al., 2020). As the share of hybrid varieties on the market is increasing (Santamaria

and Signore, 2021), research that identifies crop characteristics that are more attractive to pollinators will only grow in importance (Fijen et al., 2020).

This study focuses only on FAO crops and a few important forage crops, but there are many more crops not listed, that might be reliant on pollinators. Given the linkage of crop diversity and food security (Makate et al., 2016), future research needs to address this gap. In addition, our analysis relied solely on Scopus using English keywords, which may have limited the scope of the literature reviewed by excluding potential publications in other languages. Moreover, the study did not analyze what pollinators were observed visiting the respective crop, which could be a potential next step for future research, especially in the context of analyzing the efficiency of different pollinator species in pollinating a crop (Marzinzig et al., 2018) and being able to identify how pollination services are provided by commercial and wild pollinators respectively (Reilly et al., 2024).

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 why we followed the simple approach of calculating means for the SDRs. 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 (Balfour et al., 2022).

Lastly, we want to highlight that the raw SDR calculated here should be used with great caution as they are derived from a small number of studies, with greatly varying experimental setups. The experimental setups, like soil properties, pest control, or input use, seem to influence the effect pollinators have on the yield of a crop (Tamburini et al., 2019; Fijen et al., 2020) making SDRs most likely context-dependent. In addition, many of the identified studies only reported the weight of seeds but not the maturity of the seeds, which is important information, as some crops could have only produced immature seeds and not mature seeds. The studies that report the germinability of the seeds address this issue to some degree. Given the large number of studies that only report the seed weight but neither the maturity nor the germinability, we want to highlight that this important factor is often lacking from studies.⁶ Furthermore, given limited information we were not able to calculate the SDR for all crops based on the same metrics as sometimes only seed numbers or the total yield were reported. It is therefore recommended to work with the SDR and DR categories (Table 1) as they give a good range of where the potential real SDR lies. For future research, the interactions between treatments such as pollinators, fertilizers, and pesticide use should be examined across a wider range of relevant crops, as these studies offer valuable information to seed producers and farmers. In addition, studies that focus on organic agriculture are also relatively rare in pollinator exclusion experiments, a research gap that should provide valuable information to a growing organic sector. Public databases such as CropPol (Allen-Perkins et al., 2022) can further facilitate our knowledge of the role of pollination services in agricultural systems and help synthesize knowledge from many pollinator exclusion experiments.

5. Conclusions

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 seed dependence ratios is vital for assessing the potential risks associated

with changing pollinator populations. This study sheds light on the underestimated double dependence of certain crops, where 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 of technology and alternative pollination methods warrants 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 relationship between pollinators, seed production, and food security, highlighting the urgency of protecting and preserving these essential contributors to our food supply.

Funding

Open Access funding was facilitated and organized by Projekt DEAL. This research was supported by the German Federal Ministry of Education and Research (BMBF) under Grant Agreement No. 01UU2201A for the BEATLE project, as part of its Social-Ecological Research funding priority.

CRediT authorship contribution statement

Arndt Feuerbacher: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. Simone Melder: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Data curation, Conceptualization. Falk Krumbe: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT and Copilot to improve language and readability. After using these services, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The authors thank the editor and anonymous reviewers for their valuable comments and suggestions on earlier versions of this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109745.

References

Vallecillo, S., La Notte, A., Polce, C., Alexandris, N., Ferrini, S., Maes, J., 2018. Ecosystem services accounting. In: Part I, Outdoor recreation and crop pollination. Publications Office of the European Union, Luxembourg. https://doi.org/10.2760/619793.

⁶ Differentiating between mature and immature seeds is very difficult, as the seeds of many crops are quite small and are sometimes harvested before the fruit containing the seeds reaches full maturity.

- Allen-Perkins, A., Magrach, A., Dainese, M., Garibaldi, L.A., Kleijn, D., Rader, R., Reilly, J.R., Winfree, R., Lundin, O., McGrady, C.M., Brittain, C., Biddinger, D.J., Artz, D.R., Elle, E., Hoffman, G., Ellis, J.D., Daniels, J., Gibbs, J., Campbell, J.W., Brokaw, J., Wilson, J.K., Mason, K., Ward, K.L., Gundersen, K.B., Bobiwash, K., Gut, L., Rowe, L.M., Boyle, N.K., Williams, N.M., Joshi, N.K., Rothwell, N., Gillespie, R.L., Isaacs, R., Fleischer, S.J., Peterson, S.S., Rao, S., Pitts-Singer, T.L., Fijen, T., Boreux, V., Rundlöf, M., Viana, B.F., Klein, A.-M., Smith, H.G., Bommarco, R., Carvalheiro, L.G., Ricketts, T.H., Ghazoul, J., Krishnan, S. Benjamin, F.E., Loureiro, J., Castro, S., Raine, N.E., de Groot, G.A., Horgan, F.G., Hipólito, J., Smagghe, G., Meeus, I., Eeraerts, M., Potts, S.G., Kremen, C., García, D., Miñarro, M., Crowder, D.W., Pisanty, G., Mandelik, Y., Vereecken, N.J., Leclercq, N., Weekers, T., Lindstrom, S.A.M., Stanley, D.A., Zaragoza-Trello, C., Nicholson, C.C., Scheper, J., Rad, C., Marks, E.A.N., Mota, L., Danforth, B., Park, M., Bezerra, A.D.M., Freitas, B.M., Mallinger, R.E., Oliveira da Silva, F., Willcox, B., Ramos, D.L., da Silva e Silva, F.D., Lazaro, A., Alomar, D., González-Estévez, M.A., Taki, H., Cariveau, D. P., Garratt, M.P.D., Nabaes Jodar, D.N., Stewart, R.I.A., Ariza, D., Pisman, M., Lichtenberg, E.M., Schüepp, C., Herzog, F., Entling, M.H., Dupont, Y.L., Michener, C. D., Daily, G.C., Ehrlich, P.R., Burns, K.L.W., Vilà, M., Robson, A., Howlett, B., Blechschmidt, L., Jauker, F., Schwarzbach, F., Nesper, M., Diekötter, T., Wolters, V., Castro, H., Gaspar, H., Nault, B.A., Badenhausser, I., Petersen, J.D., Tscharntke, T., Bretagnolle, V., Willis Chan, D.S., Chacoff, N., Andersson, G.K.S., Jha, S., Colville, J. F., Veldtman, R., Coutinho, S.S., Bianchi, F.J.J.A., Sutter, L., Albrecht, M., Jeanneret, P., Zou, Y., Averill, A.L., Saez, A., Sciligo, A.R., Vergara, C.H., Bloom, E. H., Oeller, E., Badano, E.I., Loeb, G.M., Grab, H., Ekroos, J., Gagic, V., Cunningham, S.A., Åström, J., Cavigliasso, P., Trillo, A., Classen, A., Mauchline, A.L., Montero-Castaño, A., Wilby, A., Woodcock, B.A., Sidhu, C.S., Steffan-Dewenter, I., Vogiatzakis, I.N., Herrera, J.M., Otieno, M., Gikungu, M.W., Cusser, S.J., Nauss, T., Nilsson, L., Knapp, J., Ortega-Marcos, J.J., González, J.A., Osborne, J.L., Blanche, R., Shaw, R.F., Hevia, V., Stout, J., Arthur, A.D., Blochtein, B., Szentgyorgyi, H., Li, J., Mayfield, M.M., Woyciechowski, M., Nunes-Silva, P., Halinski de Oliveira, R., Henry, S., Simmons, B.I., Dalsgaard, B., Hansen, K., Sritongchuay, T., O'Reilly, A.D., Chamorro García, F.J., Nates Parra, G., Magalhães Pigozo, C., Bartomeus, I., 2022. CropPol: a dynamic, open and global database on crop pollination. Ecology 103, e3614. https://doi.org/10.1002/ecy.3614.
- Balfour, N.J., Castellanos, M.C., Goulson, D., Philippides, A., Johnson, C., 2022. DoPI: the database of pollinator interactions. Ecology 103, e3801. https://doi.org/ 10.1002/ecv.3801.
- Banerjee, O., Cicowiez, M., Macedo, M.N., Malek, Ž., Verburg, P.H., Goodwin, S., Vargas, R., Rattis, L., Bagstad, K.J., Brando, P.M., Coe, M.T., Neill, C., Damiani Marti, O., Murillo, J.Á., 2022. Can we avert an Amazon tipping point? The economic and environmental costs. Environ. Res. Lett. 17, 125005. https://doi.org/10.1088/1748-9326/aca3b8.
- Beri, S.M., Sohoo, M.S., Sharma, H.L., 1985. Mode of pollination and seed setting in Egyptian clover. Euphytica 34, 745–750. https://doi.org/10.1007/BF00035412.
- Cely-Santos, M., Lu, F., 2019. Intersections between rural livelihood security and animal pollination in Anolaima, Colombia. Geoforum 104, 13–24. https://doi.org/10.1016/ i.geoforum.2019.06.002.
- Cooley, H., Vallejo-Marín, M., 2021. Buzz-pollinated crops: a global review and metaanalysis of the effects of supplemental bee pollination in tomato. J. Econ. Entomol. 114, 505–519. https://doi.org/10.1093/jee/toab009.
- Dangles, O., Casas, J., 2019. Ecosystem services provided by insects for achieving sustainable development goals. Ecosyst. Serv. 35, 109–115. https://doi.org/ 10.1016/j.ecoser.2018.12.002.
- Debnath, S.C., 2013. Propagation strategies and genetic fidelity in strawberries. Int. J. Fruit. Sci. 13, 3–18. https://doi.org/10.1080/15538362.2012.696520.
- Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J., Potts, S.G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. Nat. Ecol. Evol. 5, 1453–1461. https://doi.org/10.1038/s41559-021-01534-000.
- Eeraerts, M., Chabert, S., De Vetter, L.W., Batáry, P., Ternest, J.J., Verheyen, K., Bobiwash, K., Brouwer, K., García, D., de Groot, G.A., Gibbs, J., Goldstein, L., Kleijn, D., Melathopoulos, A., Miller, S.Z., Miñarro, M., Montero-Castaño, A., Nicholson, C.C., Perkins, J.A., Raine, N.E., Rao, S., Reilly, J.R., Ricketts, T.H., Rogers, E., Isaacs, R., 2024. Pollination deficits and their relation with insect pollinator visitation are cultivar-dependent in an entomophilous crop. Agric. Ecosyst. Environ. 369, 109036. https://doi.org/10.1016/j.agee.2024.109036.
- FAO, 2023. FAOSTAT statistical database. Retrieved December 1, 2023, from https://www.FAO.org/FAOstat/en/).
- Feuerbacher, A., 2025. Pollinator declines, international trade and global food security: Reassessing the global economic and nutritional impacts. Ecol. Econ. 232, 108565. https://doi.org/10.1016/j.ecolecon.2025.108565.
- Feuerbacher, A., Herbold, T., Krumbe, F., 2024. The economic value of pollination services for seed production: a blind spot deserving attention. Environ. Resour. Econ. 87, 881–905. https://doi.org/10.1007/s10640-024-00840-7.
- Fijen, T.P.M., Morra, E., Kleijn, D., 2021. Pollination increases white and narrow-leaved lupin protein yields but not all crop visitors contribute to pollination. Agric. Ecosyst. Environ. 313, 107386. https://doi.org/10.1016/j.agee.2021.107386.
- Fijen, T.P.M., Scheper, J.A., Vogel, C., van Ruijven, J., Kleijn, D., 2020. Insect pollination is the weakest link in the production of a hybrid seed crop. Agric. Ecosyst. Environ. 290, 106743. https://doi.org/10.1016/j.agee.2019.106743.
- Franceschinelli, E.V., Ribeiro, P.L.M., Mesquita-Neto, J.N., Bergamini, L.L., Madureira de Assis, I., Elias, M.A.S., Fernandes, P.M., Carvalheiro, L.G., 2022. Importance of biotic

- pollination varies across common bean cultivars. J. Appl. Entomol. 146, 32–43. https://doi.org/10.1111/jen.12951.
- Gallai, N., Salles, J.-M., Settele, J., Vaissière, B.E., 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. 68, 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014.
- Gudowska, A., Cwajna, A., Marjańska, E., Moroń, D., 2024. Pollinators enhance the production of a superior strawberry – a global review and meta-analysis. Agric. Ecosyst. Environ. 362, 108815. https://doi.org/10.1016/j.agee.2023.108815.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS One 12, e0185809. https://doi.org/10.1371/journal.pone.0185809.
- Hiraguri, T., Shimizu, H., Kimura, T., Matsuda, T., Maruta, K., Takemura, Y., Ohya, T., Takanashi, T., 2023. Autonomous drone-based pollination system using AI classifier to replace bees for greenhouse tomato cultivation. IEEE Access 11, 99352–99364. https://doi.org/10.1109/ACCESS.2023.3312151.
- Hünicken, P.L., Morales, C.L., Aizen, M.A., Anderson, G.K.S., García, N., Garibaldi, L.A., 2021. Insect pollination enhances yield stability in two pollinator-dependent crops. Agric. Ecosyst. Environ. 320, 107573. https://doi.org/10.1016/j.agee.2021.107573.
- Image, M., Gardner, E., Clough, Y., Smith, H.G., Baldock, K.C.R., Campbell, A., Garratt, M., Gillespie, M.A.K., Kunin, W.E., McKerchar, M., Memmott, J., Potts, S.G., Senapathi, D., Stone, G.N., Wackers, F., Westbury, D.B., Wilby, A., Oliver, T.H., Breeze, T.D., 2022. Does agri-environment scheme participation in England increase pollinator populations and crop pollination services? Agric. Ecosyst. Environ. 325, 107755. https://doi.org/10.1016/j.agee.2021.107755.
- ISF, International Seed Federation, 2022. Seed exports 2020. Retrieved April 1, 2024, from (https://worldseed.org/document/seed-exports-2020/).
- Jing, S., Kryger, P., Boelt, B., 2021. Review of seed yield components and pollination conditions in red clover (*Trifolium pratense* L.) seed production. Euphytica 217, 69. https://doi.org/10.1007/s10681-021-02793-0.
- Johnson, J.A., Baldos, U.L., Corong, E., Hertel, T., Polasky, S., Cervigni, R., Roxburgh, T., Ruta, G., Salemi, C., Thakrar, S., 2023. Investing in nature can improve equity and economic returns. Proc. Natl. Acad. Sci. 120, e2220401120. https://doi.org/ 10.1073/pnas.2220401120.
- de Jong, N.W., van der Steen, J.J.M., Smeekens, C.C., Blacquière, T., Mulder, P.G.H., van Wijk, R.G., de Groot, H., 2006. Honeybee interference as a novel aid to reduce pollen exposure and nasal symptoms among greenhouse workers allergic to sweet bell pepper (*Capsicum annuum*) pollen. Int. Arch. Allergy Immunol. 141, 390–395. https://doi.org/10.1159/000095466.
- Klein, A.-M., Boreux, V., Fornoff, F., Mupepele, A.-C., Pufal, G., 2018. Relevance of wild and managed bees for human well-being. Curr. Opin. Insect Sci. 26, 82–88. https://doi.org/10.1016/j.cois.2018.02.011.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. Biol. Sci. 274, 303–313. https://doi.org/10.1098/ rspb.2006.3721.
- Lippert, C., Feuerbacher, A., Narjes, M., 2021. Revisiting the economic valuation of agricultural losses due to large-scale changes in pollinator populations. Ecol. Econ. 180, 106860, https://doi.org/10.1016/j.ecolegop.2020.106860
- 180, 106860. https://doi.org/10.1016/j.ecolecon.2020.106860.

 Makate, C., Wang, R., Makate, M., Mango, N., 2016. Crop diversification and livelihoods of smallholder farmers in Zimbabwe: adaptive management for environmental change. SpringerPlus 5, 1135. https://doi.org/10.1186/s40064-016-2802-4.
- Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (*Vicia faba* L.) differ in their foraging behaviour and pollination efficiency. Agric. Ecosyst. Environ. 264, 24–33. https://doi.org/10.1016/j.agee.2018.05.003.
- McGuire, S., Sperling, L., 2016. Seed systems smallholder farmers use. Food Secur. 8, 179–195. https://doi.org/10.1007/s12571-015-0528-8.
- Natural Capital Project, 2025. InVEST 3.16.0a1. Stanford University, University of Minnesota, Chinese Academy of Sciences, The Nature Conservancy, World Wildlife Fund, Stockholm Resilience Centre and the Royal Swedish Academy of Sciences. https://doi.org/10.60793/natcap-invest-3.16.0.
- Pekas, A., de Craecker, I., Boonen, S., Wäckers, F.L., Moerkens, R., 2020. One stone; two birds: concurrent pest control and pollination services provided by aphidophagous hoverflies. Biol. Control 149, 104328. https://doi.org/10.1016/j. biocontrol.2020.104328.
- R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. (https://www.R-project.org/).
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipolito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W.,
 Nilsson, L., Pattemore, D.E., Krishnan, N. de O., Pisanty, G., Potts, S.G., Reemer, M., Runlöff, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F.,
 Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. Proc. Natl. Acad. Sci. 113, 146–151. https://doi.org/10.1073/pnas.1517092112.
- Ramírez-Francel, L.A., García-Herrera, L.V., Losada-Prado, S., Reinoso-Flórez, G., Sánchez-Hernández, A., Estrada-Villegas, S., Guevara, G., 2022. Bats and their vital ecosystem services: a global review. Integr. Zool. 17, 2–23. https://doi.org/10.1111/ 1749-4877.12552.

- Regan, E.C., Santini, L., Ingwall-King, L., Hoffmann, M., Rondinini, C., Symes, A., Taylor, A., Butchart, S.H.M., 2015. Global trends in the status of bird and mammal pollinators. Conserv. Lett. 8, 397–403. https://doi.org/10.1111/conl.12162.
- Reilly, J., Bartomeus, I., Simpson, D., Allen-Perkins, A., Garibaldi, L., Winfree, R., 2024.
 Wild insects and honey bees are equally important to crop yields in a global analysis.
 Glob. Ecol. Biogeogr. 33, e13843. https://doi.org/10.1111/geb.13843.
- Ricketts, T.H., Lonsdorf, E., 2013. Mapping the margin: comparing marginal values of tropical forest remnants for pollination services. Ecol. Appl. 23, 1113–1123. https://doi.org/10.1890/12-1600.1.
- Rodger, J.G., Bennett, J.M., Razanajatovo, M., Knight, T.M., van Kleunen, M., Ashman, T.-L., Steets, J.A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L.A., Burns, J.H., Durka, W., Freitas, L., Kemp, J.E., Li, J., Pauw, A., Vamosi, J.C., Wolowski, M., Xia, J., Ellis, A.G., 2021. Widespread vulnerability of flowering plant seed production to pollinator declines. Sci. Adv. 7, eabd3524. https://doi.org/ 10.1126/cciady.abd3524
- Rohatgi, A.2024. *WebPlotDigitizer* (Version v4). Retrieved April 01, 2024, from (https://automeris.io/WebPlotDigitizer.html).
- Santamaria, P., Signore, A., 2021. How has the consistency of the common catalogue of varieties of vegetable species changed in the last ten years? Sci. Hortic. 277, 109805. https://doi.org/10.1016/j.scienta.2020.109805.
- Schurr, L., Masotti, V., Geslin, B., Gachet, S., Mahé, P., Jeannerod, L., Affre, L., 2022. To what extent is fennel crop dependent on insect pollination? Agric. Ecosyst. Environ. 338, 108047. https://doi.org/10.1016/j.agee.2022.108047.

- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3.
- Siopa, C., Carvalheiro, L.G., Castro, H., Loureiro, J., Castro, S., 2024. Animal–pollinated crops and cultivars—a quantitative assessment of pollinator dependence values and evaluation of methodological approaches. J. Appl. Ecol. 61, 1279–1288. https://doi. org/10.1111/1365-2664.14634.
- Smith, M.R., Singh, G.M., Mozaffarian, D., Myers, S.S., 2015. Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. Lancet 386, 1964–1972. https://doi.org/10.1016/S0140-6736(15)61085-6.
- Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W.H., Marini, L., 2019.
 Pollination contribution to crop yield is often context-dependent: a review of experimental evidence. Agric. Ecosyst. Environ. 280, 16–23. https://doi.org/10.1016/j.agee.2019.04.022.
- Tantau, T., 2023. The TikZ and PGF Packages: Manual for Version 3.1.10. Retrieved from (https://github.com/pgf-tikz/pgf).
- Wietzke, A., Westphal, C., Gras, P., Kraft, M., Pfohl, K., Karlovsky, P., Pawelzik, E., Tscharntke, T., Smit, I., 2018. Insect pollination as a key factor for strawberry physiology and marketable fruit quality. Agric. Ecosyst. Environ. 258, 197–204. https://doi.org/10.1016/j.agee.2018.01.036.
- Wurz, A., Grass, I., Tscharntke, T., 2021. Hand pollination of global crops a systematic review. Basic Appl. Ecol. 56, 299–321. https://doi.org/10.1016/j.baae.2021.08.008.