Animal pollinated crops and cultivars – a quantitative assessment of Pollinator Dependence values and evaluation of methodological approaches

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Abstract

Crop pollinator dependence (PD) values are key when assessing a pollinator's contribution to agriculture, guiding management plans and policies for sustainable crop production. However, available global compilations of crops PD are outdated and neglect variability between accessions (variety/cultivar) and pollen limitation (PL), i.e. the production lost due to inadequate pollen receipt.

Here, we obtained quantitative PD values for animal pollinated crops and their accessions, using data from available pollination experiments worldwide. We also tested pollination methodologies to assess their impact in PD values and to define suitable methodological guidelines for future pollination studies.

We provide a list of continuous PD values for 141 crops, including 317 accessions and 37 crops not listed in previous assessments. We found that globally, 75% of the animal pollinated crops depend highly on pollinators, with more than 40% of their production being associated with animal pollination. Pollen limitation was detected in 52% of the dataset entries, indicating that estimates calculated with open pollination studies underestimate crop pollinator dependence and so fail to represent the true pollinator contribution to food production.

The quantitative data provided here enables a more accurate estimation of pollinator contribution to food production, thus, future studies may use these values for better assessments of the value of pollinators for food security at local, regional and global scales. Additionally, future crop pollination studies should consider crop accessions and include pollen supplementation treatments for a more accurate assessment of the contribution animal pollination makes.

Keywords: Agriculture, animal pollinator dependence, crop yield, ecosystem service, hand pollen supplementation, pollen limitation, pollination.

Introduction

Biotic pollination is a crucial biodiversity-dependent ecosystem service that contributes to crop yield, supports food security, and provides other ecosystem services (Dicks et al., 2021; Power, 2010). Together with managed pollinators, diverse and abundant wild pollinator communities ensure the reproduction of pollinator-dependent crops, increasing yields and/or improving the quality of fruit and seeds, even in self-compatible crops (Klatt et al., 2014; Klein et al., 2003). Unfortunately, there is evidence that pollinator numbers are on the declining, driven primarily by human-induced changes, and pollination services may be at risk, with implications to food security and human well-being (Potts, Imperatriz-Fonseca, et al., 2016; Dicks et al., 2021).

The ability of a given crop field to achieve its maximum production potential depends on numerous environmental factors, such as nutrient and water availability, biotic interactions, and pest levels (Licker et al., 2010). For pollinator-dependent plant crops that have as their primary product fruits or seeds, pollination is directly linked with crop yield. In these crops, yield is mainly the result of two components (Fig. 1): (1) crop auto-pollination ability (the ability to produce fruits and/or seeds in the absence of pollination vectors, Fig. 1 - AUTO bar) and (2) pollination services available in each place and time (open pollination, Fig. 1 - OPEN bar). Altogether, they result in yields that, in optimal conditions, are theoretically equal to (3) the production under optimal levels of pollination (Fig. 1 - OPT bar).

The difference between open and optimal yields is known as pollen limitation (PL; Fig. 1), and it is caused by insufficient and/or inefficient pollination services (Bartomeus et al., 2014; Toledo-Hernández et al., 2017). Following Liebig's law (Liebig, 1840), crop yield is determined by the most limiting factor. In pollinator-dependent crops, when no other factors limit yield (as expected in optimized agricultural systems), pollination service may be the limiting factor (Tamburini et al., 2019). PL leads to reduced productivity through a quantitative reduction in the amount of a crop produced and/or a loss in crop quality (Vaissière et al. 2011).

The contribution of animal pollinators to crop yields (Fig. 1) can vary significantly due to spatial, temporal, and biotic factors (Bishop & Nakagawa, 2021; Mallinger et al., 2021; Webber et al., 2020). Pollinator communities are largely impacted by factors such as regional biodiversity, landscape structure, environmental conditions during flowering, and local management practices (Holland et al., 2017; Mota et al., 2022; Potts et al., 2010; Senapathi et al., 2017) and, consequently, pollination services provided by pollinator communities are likely to show significant variation.

The relative difference in yield resulting from crop auto-pollination ability and optimal pollination corresponds to the potential pollinator's contribution to production, i.e. the true level of PD, a metric highly used to endorse the importance of pollinators to humans (Fig. 1). Estimates of pollinator's contribution to agricultural production can guide both farm management practices and policymaking regarding pollinator conservation (Potts, Ngo, et al., 2016). PD values are tools to guide farmers towards practices that enhance pollinator communities, benefiting crop yield. For crops highly reliant on animal pollinators, implementing management strategies tailored to protect, sustain and, if needed, attract pollinators to the crop field becomes essential. These strategies typically prioritize the reduction of agrochemicals usage and the promotion of floral resources, habitat connectivity and nesting sites (Mota et al. 2022; Bartomeus et al. 2014; Potts et al. 2010). Furthermore, by combining crops' PD with their economic value, we can assess the direct economic impact of pollinators on crop production and crop markets (Gallai et al., 2009; Potts, Imperatriz-Fonseca, et al., 2016; Silva et al., 2021).

Studies such as Free (1993) and Klein et al. (2007) widely assessed pollinator's dependence of crops. Klein et al. (2007), the most comprehensive and widely used study, compiled PD values in four categories ("little", "modest", "high", and "essential") for 91 major global crops. This index constitutes the base for current economic assessments of pollination value at regional, national and global scales, facilitating conservation actions and initiatives focussed on pollinators and their importance (e.g. Gallai et al., 2009; Millard et al., 2023; Potts, Ngo, et al., 2016). However, due to the continuous emergence of crops and new studies being available, a revision on PD levels of crops is currently needed. Recent syntheses after the seminal work of Klein et al. (2007) include PD values for emergent crops; nevertheless, they are usually focused on a few economically important crops or specific regions of the globe (see Bishop & Nakagawa, 2021; Giannini et al., 2015; Mallinger et al., 2021). Additionally, within a crop, different accessions (plants that share similar and/or selected traits, including cultivars, varieties and other infraspecific taxonomic levels) may differ greatly in self-compatibility and auto-pollination ability (e.g. Kendall et al., 2020; Klatt et al., 2014) and, hence, different PD levels are expected (e.g. Bishop & Nakagawa, 2021; Carvalheiro et al., 2010; Marini et al., 2015). However, detailed information about PD levels in crop's accessions is scattered in the literature, making it difficult to compile, and to our knowledge, it is seldom accounted for in global studies.

Despite the growing availability of studies quantifying PD, there are challenges with the currently used methodologies, which could be underrepresenting the importance of pollinators and their associated economic value. Crops' PD literature usually evaluates crop production after open pollination (i.e. pollination provided by locally available pollinator communities), comparing it with the output after pollinator exclusion (Fig. 1). Consequently, PD values using open pollination will vary according to the local pollinator communities. Hence, we propose that hand pollen supplementation is more suitable to estimate PD since open pollination may lead to underestimations of PD values. For example, for the same plant species, a PD estimation based on an open pollination reference, in an impoverished landscape with unfavourable conditions for pollinators will generate lower PD values than a similar experiment run in a landscape with rich and abundant pollinator communities able to provide suitable pollination services. Because PL is common in wild plants and crops (Bennett et al., 2018; Olhnuud et al., 2022; Potts, Ngo, et al., 2016; Sáez et al., 2022), we expect lower estimates of PD using open pollination than with hand-pollination. Moreover, as flower manipulations may affect flower and fruit development (e.g. Hedhly et al., 2009), we expect different methodologies associated with hand pollen supplementations (e.g. emasculation and/or bagging of flowers) to impact PD estimates negatively. In contrast, experiments conducted on a smaller scale, such as individual flower level, may overestimate PD levels. This can be attributed to resource allocation, where a successfully pollinated flower, such as in hand pollen supplementations, triggers a reallocation of resources, favouring higher-quality pollinations compared to other flowers of the plant (Wesselingh, 2007). Thus, PD values are expected to be higher when pollination treatments are performed at smaller scales (e.g. flower level) than at larger ones (e.g. plant level).

We gathered information on pollination experiments for animal pollinated crops to test the aforementioned expectations and propose a methodological framework to estimate the PD of crops. Finally, we provide a list of continuous PD values for animal pollinated crops, including crop accessions whenever available. We believe this list can support more accurate economic assessments of the contribution pollinators make to food production at local, regional and global scales and guide policymaking and farm management practices regarding pollinator conservation.

Material and Methods

Dataset development

To assess animal pollination's contribution to crops production, we used data focused on pollination experiments performed in agricultural contexts and open conditions, from the PolLimCrop database (unpublished data). The search was based on a list of animal pollinated plant crops from which fruit and/or seeds are used as food and goods (FAO's list of crops, available at [https://www.fao.org/faostat/en/#data/QCL (2021)]; list of taxa given in Supporting Information, "List of taxa included in the search").

To build a dataset of crops' PD, we selected studies with three treatments. First, a hand pollen supplementation treatment, where flowers were pollen supplemented to achieve optimal pollination. Second, an open pollination treatment, where flowers received pollination services naturally, from the environment. Third, a pollinator exclusion treatment, where flowers were excluded from animal pollination through caging or bagging. We retrieved the species and common names of the crop and part of the crop economically used (fruit or seed), with species name standardized using World Flora Online. From the selected studies, the following information was also extracted: 1) production results associated with pollination treatments: fruit set, fruit weight, seed set, seed number and/or seed weight; 2) data related to geographical aspects of the study, i.e. continent and country; and 3) records of the additional treatments undertaken that were supplemental to the pollination treatments. These treatments were designated: H – hand pollen supplementation, only; BH – pollinator exclusion and hand pollen supplementation; EH – emasculation and hand pollen supplementation; BEH – pollinator exclusion, emasculation and hand pollen supplementation. The scale of the pollination experiment was also noted in terms of whether the pollination treatment was applied the complete plant, branch, inflorescence (including flower clusters) or individual flower. Additional details on the characteristics of the used dataset can be found in the Supporting Information. Further details on extracted variables are provided in Table S1.

Pollinator dependence estimation

PD values were calculated using the following equation:

PD = 1 – [pollinator exclusion production / pollinator-associated production]

where *pollinator exclusion production* refers to the production in the absence of pollinators, and *pollinator-associated production* refers to the production associated with animal pollinator visitation (i.e. hand pollen supplementation or open pollination).

Where PD estimates were provided for multiple production variables, the values derived from the commercially used parts were used here (seed and/or fruit). In fruit crops, fruit-related production variables were used for PD calculation, i.e. fruit set and fruit weight. For seed crops, seed set, and seed number and weight were used, in addition to fruit set. In some cases, where both fruit and seed parts are economically used, fruit and seed-related production variables were used to calculate PD values. When several production variables were provided, a mean value of the obtained PD values was calculated and used. Two PD values were calculated for each entry, one using hand pollen supplementation and pollinator exclusion treatments (PD-SUP) and the other using open pollination and pollinator exclusion treatment (PD-OPEN). PD ranged between 0 and 1, with 0 representing a lack of PD and 1 representing the highest level.

To identify methodological problems with pollinator exclusion and hand supplementation methodologies, outliers were visually inspected. In four entries (out of

564), pollinator exclusion production was 25% higher than pollinator-associated production and were likely related with methodological problems related with the pollinator exclusion methodology. Therefore, PD values were not calculated for those four entries. For the 13 remaining entries where pollinator exclusion production was higher than pollinator-associated production, PD estimates were considered to be zero. Additionally, in 11 entries, pollen supplementation production was 25% lower than open pollination production suggesting methodological problems with the hand supplementation methodology. PD values were not calculated for those entries. To guarantee that the removal of these 15 studies did not affect the main findings of this study, the statistical analyses were performed with the entire dataset (see *Statistical analyses* section).

A final PD value was obtained for each entry (defined here as PD-final), using either hand pollen supplementation or open pollination treatment, by selecting the maximum value obtained. Variation in production variables is expected, and thus, cases where open pollination overcomes hand pollen supplementation may occur. Cases where production of open pollination are much higher than after hand pollination might reflect methodological issues or lack of efficiency or success in hand pollen supplementation; such cases may affect the data and lead to misleading conclusions. Here, entries in which PD-OPEN was 25% higher than PD-SUP were not used in statistical analyses. These represented only 11 entries (out of 564) and did not significantly affect overall conclusions (see Supporting Information). For every database entry, PD-SUP, PD-OPEN and PD-final was added to the dataset for the subsequent statistical analyses.

Statistical analyses

A total of 165 records contained hand pollen supplementation, open pollination and pollinator exclusion and were included in statistical analyses. To compare PD levels after open pollination and hand pollen supplementation, General Linear Mixed-Effects Models (GLMMs) were created using PD values from both treatments, with "treatment type" as an explanatory variable. To account for variation associated with crop identity, "crop" was included as a random variable in all models. Similarly, "article code" was also used as a random variable to remove confounding effects of within-study aspects.

To evaluate if PD values depended on specific aspects of the methodologies used, analyses were performed using PD-final obtained in our dataset. In particular, GLMMs were performed to analyse the effects of hand pollen supplementation methodology and scale of the pollination experiment on PD values. Hand pollen supplementation methodology included four techniques (see Table S3, 'supplement type'). Scale included four experimental scales (see Table S3, 'scale'). Again, "crop" and "article code" were used as random factors. GLMMs were performed using function "lmer" of the R package "lme4" (Bates et al., 2014), with logit transformation of adjusting factor of 0.01 of the R package "car" (Fox & Weisberg, 2019). Wald chi-square analyses were used to calculate the effect of tested variables on PD values. We then ran post hoc pairwise comparisons to test for differences within treatments of supplement type and scale, using R package "emmeans" (Lenth et al., 2018). All analyses were rerun with the complete dataset (including the above mentioned 15 entries) to evaluate if similar trends were observed. The studies on apples constituted 33% of PD values in all performed analyses (see Table S2, Crop "Apple"). To test if such a large set of studies on one crop influenced our results, all analyses without apple's entries were rerun.

To enable comparison with previous global studies, we grouped our continuous PD values into the classes used by Klein et al. (2007; little: 0–0.09 PD, modest: 0.10–0.39, high: 0.40–0.89, essential: 0.90–1.00). All analyses and graphs were obtained in R software (version 4.2.1).

Pollinator dependence – Compilation table

To provide a comprehensive list of PD values for animal pollinated crops and their accessions, we created a 'compilation table' (Table S2) containing the mean PD values calculated for the 165 records used in statistical analyses, and a set of 64 studies reporting only hand-pollen supplementation or open pollination (thus excluded from statistical analyses). A full list of contributing studies is given in the Supporting Information.

Mean values were obtained using PD-final from each entry available, plus PD-final of the additional studies (Table S2). Values of PD ranged from 0 to 1, with negative values being considered as 0, indicating no animal pollinator dependence. Treatments that contributed to mean PD values (either hand pollen supplementation treatment, open pollination, or both) are indicated in the dataset. Similarly, mean PD values were obtained and assembled for all the available accessions within crops (Table S3).

Results

Open pollination versus hand pollen supplementation

A total of 165 records, corresponding to 91 different crops, were used in statistical analyses, including 549 entries with PD values (representing different crops, accessions, years and experimental sites). A map with the geographical distribution of studies and entries included in data analyses is provided (Fig. 2a). A detailed list of record type (e.g. article, thesis or proceeding) are provided in the Supporting Information (Table S4). Crops with most entry values of PD were apple, oilseed rape and almond (representing 33.1%, 6.4% and 4.2% of total entries, respectively). Twenty-seven crops were represented by one value of PD only.

PD values estimated after hand pollen supplementation-associated production were significantly higher (ca. 5.7% higher on average) than those estimated after open pollination (χ^2=38.5260, P<0.0001; Fig. 2b; Table S4). Hand pollen supplementation gave higher PD values than open pollination in 51.5% of cases (Fig. 2c, Fig. S1a). Hand pollen supplementation and open pollination gave similar PD values in 23.9% of cases (Fig. 2c, Fig. S1a). Finally, hand pollen supplementation led to lower PD values than open pollination in 24.6% of cases (Fig. 2c, Fig. S1a).

Methodological considerations regarding hand pollen supplementation

No significant differences were found in PD values among pollen supplementation techniques (χ^2=4.6863, P=0.1963; Fig. S1b; Table S5). However, signs of resource allocation were observed, with significant differences in PD values among experimental scales used in pollination experiments (χ^2=8.0840, P=0.0443; Table S5). Despite these signs, no significant differences were observed among scales in post hoc tests (Fig. S1c;

Table S6). Similar results were obtained when rerunning analyses without apple studies (Tables S8-S10), and with and without the studies removed (Tables S11-S13).

Crop pollinator dependence values

Mean PD values are provided for 141 animal pollinated crops. A list of taxa with PD estimated values is given in Supporting Information (Table S2). Information on specific PD values of crop accessions (including cultivars, varieties and other infraspecific taxonomic levels) is provided for 94 crops, comprising 317 individual crop accessions (Table S3).

The mean value of PD (PD-final) across all crops of the list was 0.63 ± 0.30 (mean ± SD). Values varied, as expected, from no PD (value of 0) to complete PD (value of 1); however, a concentration of values around 1 was observed, with 27.0% of the crops having high PD values (PD ≥ 0.90) (Fig. 3a).

When considering the animal pollinator dependent classes defined by Klein et al. (2007), 74.5% of the crops were classified as “high” (67 crops, 47.5%) or “essential” (38 crops, 27.0%) (Fig. 3b), representing a higher number of crops than in Klein et al. (2007). A similar number of crops were observed in the “modest” class in both studies, here representing 19.9% of the total crops (28 crops). Contrarily, the number of crops classified as “little” was lower than in Klein et al. (2007), comprising only 5.7% of crops in our compilation (8 crops; Fig. 3b).

Discussion

Crop pollinator dependence values

This study provides a new compilation of PD values for animal pollinated crops. For several crop species, PD values given here differ from previous global assessments (Klein et al., 2007), with many crops having higher PD values than listed previously. 75% of the animal pollinated crops were categorized in PD classes "high" or "essential", an increased ratio compared with compilations such as Klein et al. (2007). Additionally, compared with previous approaches, the list comprises, for the first time, continuous PD values for 141 worldwide crops, including 317 crop accessions, estimates for 37 crops (highlighted in bold, Table S2) not listed previously or with no data in former global assessments, and detailed data for several crops that were once merged in large groups (see Fig. 4). By providing PD values discriminated for individual crop species and their accessions, our study contributes with vital and, until now, neglected information.

Several PD values of individual crops were higher than in previous compilations (e.g. *Citrus*, durian, strawberry, sunflower). These differences are mainly explained by the fact that PD values were obtained through a different methodology, here using hand pollen supplementation instead of open pollination (primary treatment used in previous estimates) to obtain final PD value. As hand pollen supplementation accounts for effects of PL, it provides more accurate measures of PD. Once PD estimations are usually based on open levels of pollination, previous studies and compilations are substantially underestimating animal pollinator's importance for crop production.

We found wide variation in the PD values reported within crops. This might be expected since the degree of self-compatibility and auto-pollination ability has been shown to vary among crop accessions (e.g. sunflower, Carvalheiro et al., 2011; oilseed rape, Hudewenz et al., 2014). Knowledge of the pollination requirements of crop accessions is crucial for suitable management decisions (Hudewenz et al., 2014), and is becoming a particularly useful in regions where pollinator loss is, or is anticipated to be, more pronounced (Potts, Ngo, et al., 2016). For example, in pollinator-impoverished locations, when pollinator communities are insufficient to provide the needed pollination services to a crop, selecting accessions that are less dependent on animal pollination may be a suitable solution to ameliorate PL. Unfortunately, 29% of the studies analysed here did not provide information about crop accessions (or any other infraspecific taxonomic level, such as cultivar, variety, forma or clone), hindering the compilation of precise data. Considering the importance of this information (Hudewenz et al., 2014), we recommend that future works should always provide information and data for each accession of the crop under study.

The optimal pollination level from the plant perspective (i.e. plant fitness) differs from that of farmers perspective (i.e. agronomic and economic yield). To follow farmers' perspective, PD value was calculated using different production variables, depending on the part of the crop economically used (fruit or seed). Quantity (e.g. fruit set) and quality (e.g. fruit weight) production traits were considered, to accurately account for the impact of animal pollination at both levels. Studies on PD often focus on quantitative variables, with mixed responses between these and qualitative variables (e.g. Bartomeus et al. 2014; Stein et al. 2017). Here, however, only 30% of the entries presented quantity and quality variables. Hence, we recommend that future experiments evaluate production variables related to both levels.

Open pollination vs. hand pollen supplementation to calculate PD values

Hand pollen supplementation led to higher PD values than open pollination in 51.5% of datapoints that had information in both treatments. These results are consistent with our predictions and indicate that PL is common, reducing yield level and, consequently, underestimating potential pollinator's contribution. Therefore, in locations where pollination services are inadequate and/or impoverished, such as landscapes of poor quality due to high levels of fragmentation and/or simplification (Aizen & Feinsinger, 2003, Nicholson et al., 2017), hand pollen supplementation is a more suitable treatment to achieve optimal crop yield and obtain an accurate estimate of PD value. However, despite the importance of accurate PD estimates to value pollinator's contribution to production systems, and even though hand pollen supplementation is widely used to study PL in wild plants (e.g. Bennett et al., 2018; Knight et al., 2005), in crops, its use for the calculation of PD has been rare (but see Bishop & Nakagawa, 2021; Garibaldi et al., 2011; Garratt et al., 2021). Based on these results, we recommend that hand pollen supplementation is included in pollination experiments that aim to assess the contribution of animal pollination to crops. A complete experimental design for such purposes is provided below and in Box 1.

Methodological guidelines for hand pollen supplementations

When performing hand pollen supplementations, assuring efficiency is critical (see Box 1). However, in plant families with complex flower structures or with flowers sensitive to manipulation, this can be challenging to achieve. In such cases, animal pollinators may perform better at pollinating than hand pollen supplementation by humans since animals are adapted to exploit floral resources. Thus, the fact that hand pollen supplementation produced lower production values in 24.6% of the data points compared with open pollination is not entirely unexpected. It is possible that in these studies, the supplementation of pollen was not ideal, or that over-pollination led to reduced yield (Bishop et al. 2020). This may represent a limitation of the dataset used in our study, which can lead to the undervaluation of PD levels. Indeed, technical approaches used in hand pollen supplementation, such as type of supplementation, scale at which pollination experiments are done and pollen source, are known to affect yield in certain crops (e.g. Webber et al., 2020).

Emasculation of flowers prior to hand pollen supplementation and bagging plants after hand pollination are practices often performed on pollination experiments to exclude production associated with auto-pollination and/or avoid undesirable external pollen, respectively (e.g. Chacoff & Aizen, 2007; Kendall et al., 2020). Here, no significant differences were obtained between standard hand pollen supplementation and supplementation with some of the techniques detailed above, indicating that supplementation using these methods provide reliable estimates of PD or, at least, estimates comparable to hand pollinations.

PD values are expected to be higher in pollination treatments conducted at smaller scales (e.g. flower level) than at higher ones (e.g. plant level), as resources for fruit/seed development are usually limited and will be preferentially (re)allocated to flowers with higher pollination quality (Webber et al., 2020). Although no significant differences were observed among different scales, higher PD values were obtained in experiments that used flower as a scale, with marginal *p*-values obtained when comparing flower vs. inflorescence scales (P=0.0762). Therefore, more research focused on resource allocation occurrence is needed to fully disentangle the impact of lower scales on associated production levels. In the meantime, studies should indicate the treatment scale and increase the scale whenever possible to avoid resource allocation problems.

Hand pollen supplementation should be included in crop pollination experiments to account for PL, providing a more accurate method to calculate PD values and assess total pollinator's contribution to crop production. Yet, it should be bear in mind that the inclusion of hand pollen supplementation increases the time and complexity of such experiments, particularly in mass flowering or self-pruning crops (where sample size needs to be significantly increased to compensate for self-pruning losses) or in plants with complex, fragile flower structures (demanding more time for hand pollen supplementations). Therefore, when designing a pollination experiment, all factors linked with crop reproductive traits should be considered (Young & Young, 1992), acknowledging the limitations and advantages of selected treatments (see Box 1).

Conclusions

This compilation offers valuable PD values at both crop and accession levels, enabling precise economic assessments for individual crops and subsequently supporting informed decisions in the management of animal pollinated crops. Our results highlight the importance of recognizing that the commonly applied method of assessing PD (comparing fruit set in plants exposed vs isolated from pollinators) can lead to underestimations of PD values. Due to this, the value of animal pollination to production of crops may be higher than previous studies established. Given that most published studies on pollinator's contribution to crops use PD values obtained through methodologies that did not account for pollen limitation, it is probable that pollinator's contribution to crops’ local and global production, international trade markets, and economic value of pollinators are substantially undervalued.

Authors’ contributions

CS, LGC and SC developed hypothesis and statistical methods, which were discussed with HC and JL. CS and HC led literature search and data extraction. CS, HC and SC performed data validation. CS wrote the first draft, and all remaining authors edited and commented on earlier versions of the manuscript.

Acknowledgements

The authors thank the anonymous reviewers and Robin Payne for their manuscript suggestions. This work was funded by the Integrated Programme of Scientific Research and Technological Development CULTIVAR (CENTRO-01-0145-FEDER-000020), co-financed by the Regional Operational Programme Centro-2020, Portugal-2020 and European Union, through ERDF. Portuguese Foundation for Science and Technology (FCT) financed CS through the fellowship SFRH/BD/145962/2019, HC through national funds by the framework contract foreseen in numbers 4-6 of article 23, Decree-Law 57/2016, and SC through the Scientific Employment Stimulus 2021.02697.CEECIND. LGC was funded by the Brazilian Conselho Nacional de Desenvolvimento Científico e Tecnológico CNPq (307625/2021-4).

Conflict of Interest

None declared.

Data accessibility statement

Additional supporting information can be found online in Supporting Information. Upon acceptance of the manuscript, data will be available via figshare, with a provided link.

Supporting Information

Supporting information can be found online in Supporting Information section.

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Figures

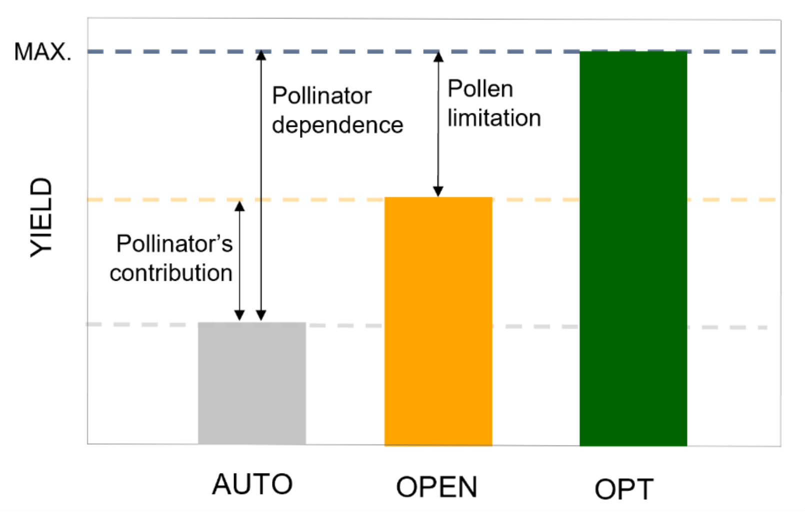
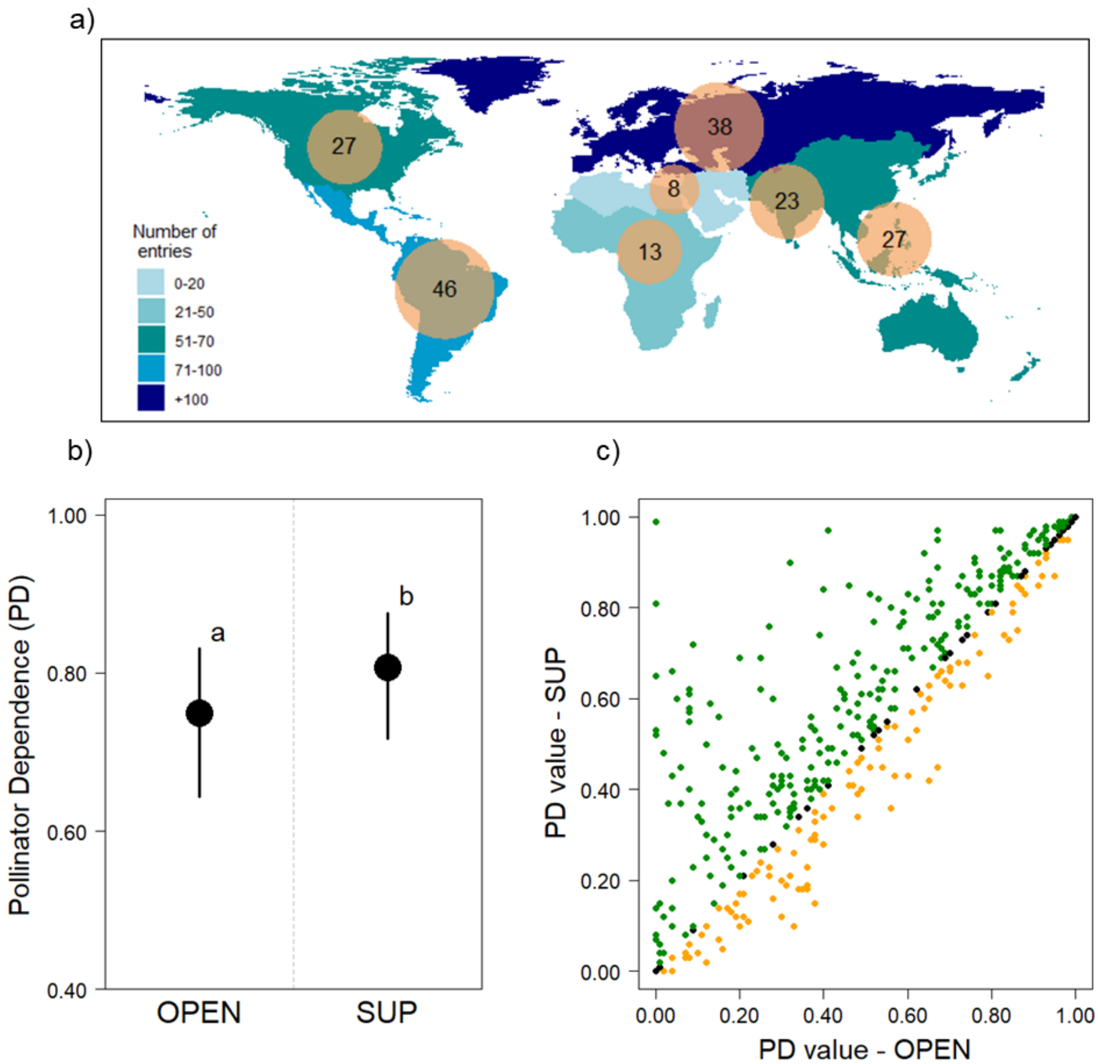


Figure 1. Theoretical representation of pollination components associated with yield in pollinator-dependent crops: autonomous self-pollination levels (AUTO), open levels of pollination (OPEN), and optimal pollination levels for local study conditions (OPT). Associated indexes are also presented: (1) **pollinator's contribution**, yield associated with existing pollination services; (2) **pollinator dependence**, yield directly dependent on pollinators (for simplification, here we considered a crop with negligible wind contribution for pollination) and (3) **pollen limitation**, yield loss associated with limited pollen deposition levels. See Box 1 for methodologies associated with estimations of each component and index.



657 Figure 2. a) Global distribution of data entries and studies of the analysed dataset. The
658 colour gradient in the map area represents the total number of entries for the different
659 regions, by ranges. Orange circles represent the total number of studies for the different
660 regions. b) Estimated means and 95% confidence interval values for PD estimates
661 obtained with open pollination (OPEN) and hand pollen supplementation (SUP)
662 treatments (χ^2=38.5260, P<0.0001). Different letters indicate significant differences at
663 P<0.05. c) Scatterplot of PD values obtained through SUP treatment (y-axis) in relation
664 to that obtained through NAT (x-axis); PD values in which PD-SUP>PD-OPEN are
665 represented as green dots, PD-SUP<PD-OPEN are represented as yellow dots and PD-
666 SUP=PD-OPEN are represented as black dots.

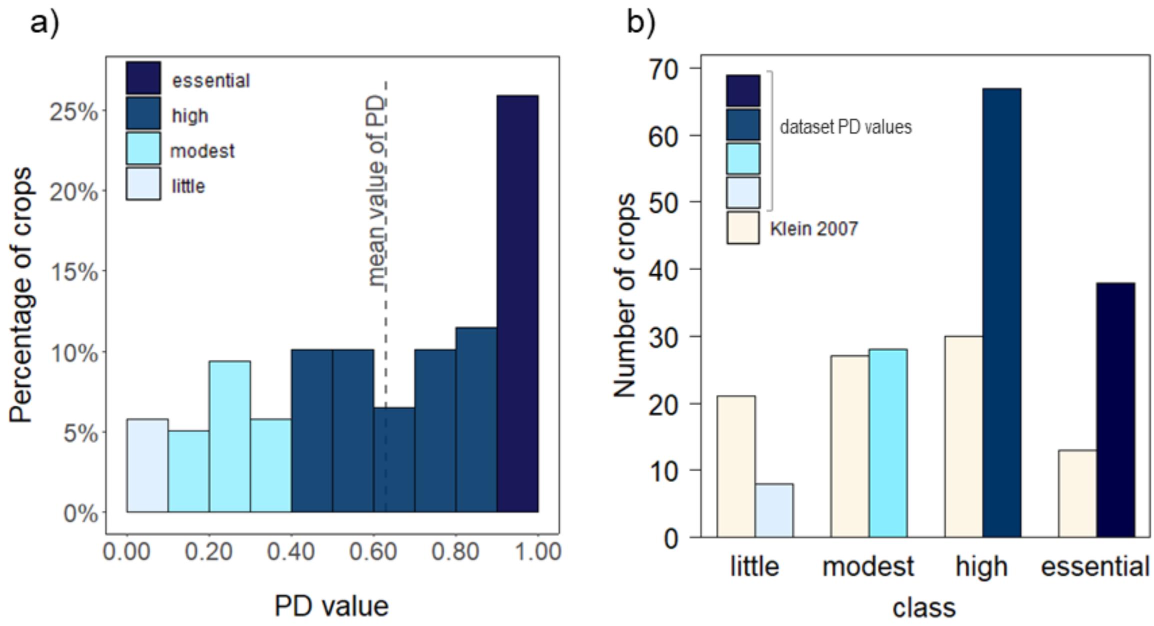


Figure 3.a) Percentage of crops along PD values (0.10 interval range). Final PD was used for each crop (values given in Table S2). Overall mean PD is indicated through a dashed line. Different colour bars represent classes as defined by Klein et al. (2007); b) Number of crops on each PD class: “little” (PD between 0-0.09), “modest” (0.10-0.39), “high” (0.40-0.89) and “essential” (0.90-1.00). Beige bars represent the crop’s distribution among classes as defined by Klein et al. (2007), and different blue bars represent crops’ distribution in this study. Classes classified as "no increase" and "unknown" in Klein et al. (2007) were excluded from our study.

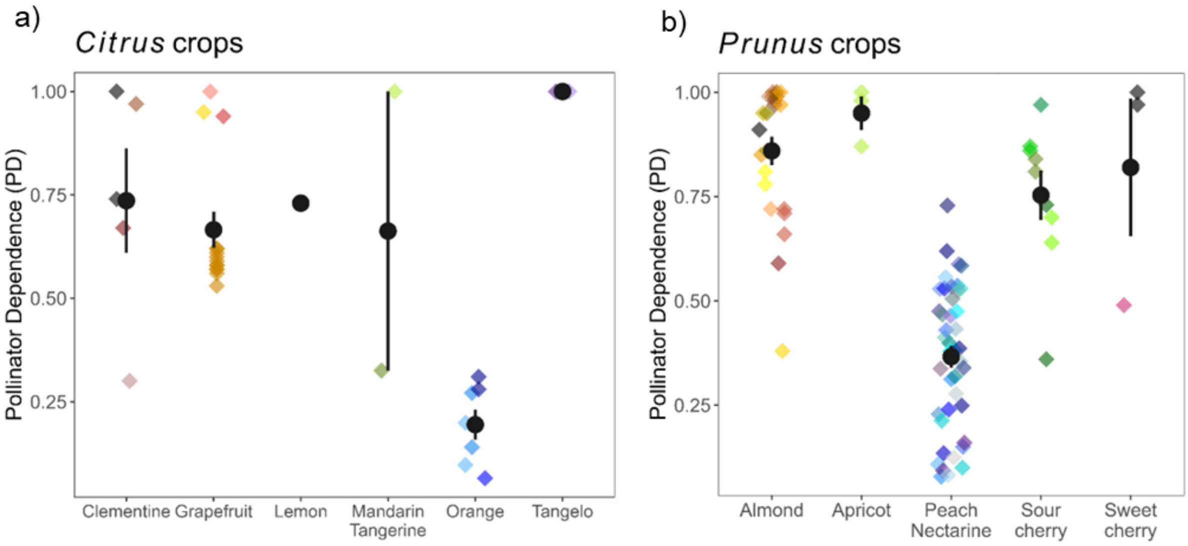


Figure 4.a) Mean ± SE values of PD for each crop within the Citrus group; b) Mean ± SE values of PD for each crop within the Prunus group. Coloured points represent individual PD values, with included accessions represented by different colours. See Tables S2 and S3 for specific data regarding PD values.

Box 1: Guidelines for pollination experiments when studying animal pollination contribution.

An experimental design should include the following treatments:

a) **pollinator exclusion:** a bagged treatment, without biotic visits. In crops also pollinated by wind, the experimental design should also evaluate its contribution using two bagging treatments, one using a mesh fabric that allows wind contribution, excluding only biotic interactions, and another using a mesh that restrains pollen movement by both wind and biotic agents. Wind contribution is given by the difference between the two bagged treatments.

b) **open pollination:** a treatment without any manipulation of the reproductive units where flowers are naturally pollinated.

c) **optimal pollination** (or pollen supplementation)**:** a treatment where flowers are naturally pollinated and to which a hand pollen supplementation is provided. Pollen applications should be performed once or multiple times, depending on the crop's requirements. The use of compatible pollen is crucial, and several sources of compatible pollen should be applied.

Additional notes:

- Bigger scales are preferred (i.e. branch or plant scales).
- Hand pollen supplementations without additional treatments, as bagging or emasculation, are advised but, if additional treatments are essential for the experiment, they can be considered.
- All relevant details should be provided (e.g., accession, cultivar), additionally to details surrounding agricultural management (e.g. application of reproductive hormones, presence of managed pollinators).