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Review

Pollination contribution to crop yield is often context-dependent: A review of experimental evidence

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ABSTRACT

Insect pollination is a well-studied ecosystem service that supports production in 75% of globally important crops. Although yield is known to be sustained and regulated by a bundle of ecosystem services and management factors, the contribution of pollination to yield has been mostly studied in isolation. Here, we compiled and reviewed research on the contribution of pollination to crop yield under different environmental conditions, where the potential interaction between pollination and other factors contributing to yield, such as nutrient availability and control of pests, was tested. Specifically, we explored whether pollination displayed synergistic, compensatory or additive effects with concomitant factors. The literature search resulted in 24 peer-reviewed studies for a total of 39 individual tests of interactions. Studies examined responses in 13 crops testing interactions both at the local and the landscape scale. Interactions between pollination and other factors influencing yield were observed for several crops and mostly displayed positive-synergistic relationships. Crop life-history traits such as pollination dependency were found to affect the plant response to variations in resource and pollen availability. Soil properties and crop pests might affect contribution of pollination to yield by altering the amount of resources a plant can allocate to reproduction, independently of the amount of pollen provided. Current management strategies to enhance pollinators might fail to increase pollination benefits in landscapes characterized by poor soil resources or ineffective pest control. We propose that our understanding of the effects of crop-pollinator interactions will benefit by focusing on plant traits and physiological responses. Combining knowledge from plant physiology and ecology with technological advances in agriculture is needed to design novel management strategies to maximize pollination benefits and support yields and reduce environmental impacts of food production.

1. Introduction: pollination benefits in agriculture

Supporting yields while minimizing negative environmental impacts of agriculture is a major challenge of our century. There are numerous biotic and abiotic factors that influence crop growth and yields, as well as their potential interactions (Lobell et al., 2009). The contribution of these factors in closing yield gaps can be enhanced by improving agronomic management (e.g. irrigation, fertilization, plant breeding, integrated pest management) and/or by integrating bundles of ecosystem services into crop production (ES, e.g. soil fertility, pest control, water retention; Bommarco et al., 2013; Kleijn et al., 2018). Finding an optimized integration of agronomic inputs and provisioning of ES is a key challenge in modern cropping systems.

Pollination is a well-studied service, supporting production in c. 75% of globally important crops (Klein et al., 2007; Garibaldi et al., 2013). Inadequate pollen deposition (i.e. pollination limitation) can limit both yield quantity and quality of several crops (e.g. Bartomeus et al., 2014; Lindström et al., 2016; Toledo-Hernández et al., 2017). The global decline in wild and managed pollinators has therefore caused concerns about potential negative impacts on food production (González–Varo et al., 2013; Vanbergen, 2013; Potts et al., 2016). Moreover, agriculture has become more pollinator dependent because of a great increase in the area cultivated with pollinator-dependent crops worldwide (Aizen et al., 2008; Breeze et al., 2011). Current

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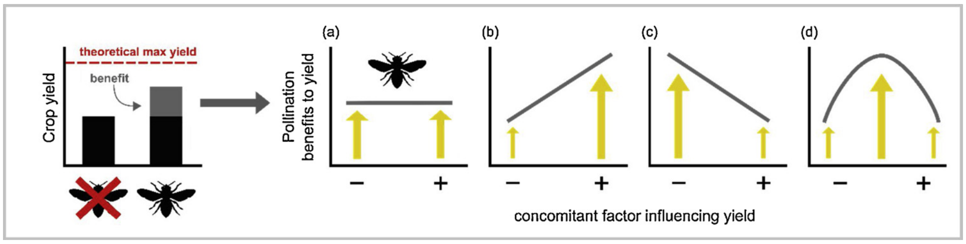

Fig. 1. Pollination benefit to crop production is defined as the yield gain directly attributable to animal pollination processes. In all situations depicted in the panels a–d, pollination benefits can vary with the provision of a concomitant factor. These factors can be either ecosystem services or management inputs affecting yield. Effects of pollination independent of the effects of concomitant factor (a). Alternatively, effects of pollination on crop yield can increase, decrease or show a unimodal relationship with the contribution of the concomitant factor involved in crop production (b, c, and d, respectively).

strategies to counteract pollination limitation in flowering crops mainly consist of interventions to improve habitats known to sustain pollinator communities (e.g. semi-natural habitats, flower strips; Winfree et al., 2009; Garibaldi et al., 2014; Riedinger et al., 2014; Pywell et al., 2015; Scheper et al., 2015). Nevertheless, pollination benefits to yield (i.e. yield gains directly attributable to animal pollination processes; Fig. 1) might not only depend on its level of provisioning (i.e. pollen deposition), but also on other natural and agronomic factors affecting plant growth (e.g. Knight et al., 2005; Bos et al., 2007). It is, therefore, important to understand the potential context-dependence of pollination benefits.

Seed production in flowering crops is principally driven by the availability of resources and/or pollen transfer. Different ES and management practices can greatly affect resource availability to crop development (Zhang et al., 2007; Power, 2010), altering therefore the amount of resources a plant can allocate to reproduction (Bloom et al., 1985). Since pollination processes are intrinsically linked to plant physiology (Knight et al., 2005), pollination benefits to yield might change at different levels of resource availability. Theoretical models predict that the degree of pollen limitation is greater at higher levels of resource availability (Haig and Westoby, 1988; Burd, 2008). In fact, when flower production and seed/fruit maturation processes are maximized, pollen availability remains the main factor limiting yield. Nevertheless, specific crop characteristics can also modify the interplay between resource availability deposition and yield. Crop life-history traits such as pollination dependency, flowering pattern, and life span are expected to shape the impact of resource availability on pollination benefits (Knight et al., 2005; Wesselingh, 2007). Hence, interactions between pollination, crop management and other ES may occur in different forms (Garibaldi et al., 2018). First, pollination benefits might increase when the contribution of the other factors increases, exhibiting a synergistic relationship (Fig. 1b; Burd, 2008). Second, pollination benefits might decrease with increasing contribution of concomitant factors compensating, to some extent, for the limited contribution to yield of the other factor (Fig. 1c; Wesselingh, 2007). Third, pollination benefits might also be maximized at intermediate levels of the concomitant factor (Fig. 1d).

An emerging interest in the management of multiple ES for productive and sustainable farming (Bommarco et al., 2013) has motivated an increasing number of studies of interactions between pollination and both management and ES (Garibaldi et al., 2018). The time is ripe to make a synthesis of the available empirical evidence. The objective of this review is to summarize the current knowledge regarding interactions between pollination and concomitant management as well as some natural factors influencing crop production and to explore the potential mechanisms driving these processes. We tested the hypothesis that (i) the benefits of pollination to crop yield are often context-dependent and the contribution of multiple ES and management factors are only rarely additive; (ii) crop life-history traits influence the emergence and the type of interactions. Since the number of potential interactions is high compared to the available primary data and it is not straightforward to analyse interactions in meta-analyses, we performed a qualitative synthesis of the available literature. This could provide a starting point to analyse emerging patterns to steer and facilitate future research in this complex but important field of applied ecological research.

2. Methods: literature review and dataset investigation

We conducted a literature review consulting the online reference database ISI Web of Science (for details about selection criteria and process see Fig. S1). We selected all peer-reviewed studies where yield response to insect pollination (pollination benefits) was measured in crops and related to the experimental manipulation of at least one other concomitant ES or management factor below and/or above ground. Concomitant ES and management factors were usually quantified as the beneficial effects they produced on yield (e.g. low pest density for pest control, high nutrients for soil fertility or fertilization). The distinction between the effects of ES and management factors on yield are often subtle: fertilization or irrigation effects on crop, for instance, can be related to situations with high provisioning of soil services, such as efficient nutrient cycling or water retention. We therefore did not differentiate between the effects of enhanced ES provisioning and management practices. Non-manipulative surveys that avoided collinearity among ES and management factors were also included, while we did not consider studies mapping synergies and trade-offs based on spatial correlation (e.g. Mitchell et al., 2014). We therefore described 24 studies in our review (39 tests, Fig. S1).

To reliably explore combined effects of pollination and other factors on yield, we first excluded analyses that reported one or more non-significant main effects and at the same time showed a non-significant interaction (Fig. S1). If even one of the main effects is not relevant to crop production it is not logical to examine whether these factors have additive or interacting effects. Non-significant main effects might happen when the factors considered are not relevant for yield production or the gradient explored is not broad enough to produce an effect (e.g. rainfall exclusion on cacao production, Groeneveld et al., 2010; hand vs. natural pollination in cucumber, Barber et al., 2012). Secondly, we removed three studies (five tests) that did not report reliable measures of yield but only of yield parameters (e.g. weight per fruit but not total fruit weight per plant, Hladun and Adler, 2009; 19 included studies, 24 tests). Considering the net effect of interactions on final production is in fact essential to design efficient management strategies that are relevant for farmers. Finally, for this subset of studies, we explored how different crop life history traits (pollination dependency, life span and flowering strategy, Table S1) affected the significance of emerged interactions.

3. General trends

First, we present the general patterns that emerged from the selected literature. Second, we discuss individual studies for soil factors and pest control, separately. Third, we explore the potential mechanisms driving interactions between pollination and concomitant factors.

Table 1
Interactions between pollination and concomitant factors influencing yield investigated in this review (39 tests from 24 studies). Type of experiment: field or pot, experiments performed in open field or with pots – local or landscape, experiments performed in one location or in multiple locations selected along a landscape gradient. Type of interaction (see Fig. 1; inclusion based on selection criteria; Fig. S1). AB, aboveground. Complete table in the Supplementary Material (Table S2).

	Reference	Concomitant factor explored	Crop	Type of experiment	Type of interaction (Fig. 1)
1	Al-Kahtani et al., 2017	phosphorus availability	alfalfa	field - local	b
2	Bartomeus et al., 2015	soil fertility	oilseed rape	field - landscape	-
3	Bartomeus et al., 2015	soil fertility	oilseed rape	field - landscape	a
4	Bartomeus et al., 2015	soil fertility	oilseed rape	field - landscape	a
5	Bartomeus et al., 2015	florivorous pest	oilseed rape	field - landscape	c
6	Boreux et al., 2013	nutrient availability	coffee	field - landscape	a
7	Boreux et al., 2013	water availability	coffee	field - landscape	a
8	Forbes and Northfield, 2017	nutrient availability	cacao	field - local	c
9	Garratt et al., 2018	nutrient availability	oilseed rape	pot - local	b
10	Grass et al., 2018	AG pest control	wild mustard	pot - landscape	b
11	Klein et al., 2015	water availability	almond	field - local	b
12	Lundin et al., 2013	seed herbivory	red clover	pot - landscape	b
13	Marini et al., 2015	nitrogen availability	oilseed rape	field - local	c
14	Melathopoulos et al., 2014	AB pest control	blueberry	field - local	b
15	Motzke et al., 2015	nitrogen availability	cucumber	field - landscape	a
16	Motzke et al., 2015	weed control	cucumber	field - landscape	b
17	Perrot et al., 2018	phosphorus availability	oilseed rape	field - landscape	a
18	Ramos et al., 2018	nitrogen availability	faba bean	field - landscape	c
19	St–Martin and Bommarco, 2016	soil fertility	faba bean	pot - local	b
20	Strauss and Murch, 2004	leaf herbivory	cantaloupe	field - local	c
21	Sutter and Albrecht, 2016	florivorous pest	oilseed rape	field - local	b
22	Tamburini et al., 2016a	soil fertility	sunflower	pot - local	b
23	Tamburini et al., 2017	nitrogen availability	sunflower	field - local	d
24	Van Gils et al., 2016	nitrogen availability	oilseed rape	pot - landscape	a
25	Van Gils et al., 2016	AB pest control	oilseed rape	pot - landscape	b
26	Barber et al., 2011	leaf herbivory	cucumber	field - local	not included
27	Barber et al., 2011	root herbivory	cucumber	field - local	not included
28	Barber et al., 2012	leaf herbivory	cucumber	field - local	not included
29	Bartomeus et al., 2015	nitrogen availability	oilseed rape	field - landscape	not included
30	Boreux et al., 2013	soil fertility	coffee	field - landscape	not included
31	Classen et al., 2014	AB pest control	coffee	field - local	not included
32	Forbes and Northfield, 2017	AG pest control	cacao	field - local	not included
33	Groeneveld et al., 2010	nitrogen availability	cacao	field - local	not included
34	Groeneveld et al., 2010	water availability	cacao	field - local	not included
35	Hladun and Adler, 2009	leaf herbivory	pumpkin	field - local	not included
36	Hladun and Adler, 2009	root herbivory	pumpkin	field - local	not included
37	Klein et al., 2015	nutrient availability	almond	field - local	not included
38	Motzke et al., 2015	AB pest control	cucumber	field - landscape	not included
39	Van Gils et al., 2016	soil fertility	oilseed rape	pot - landscape	not included

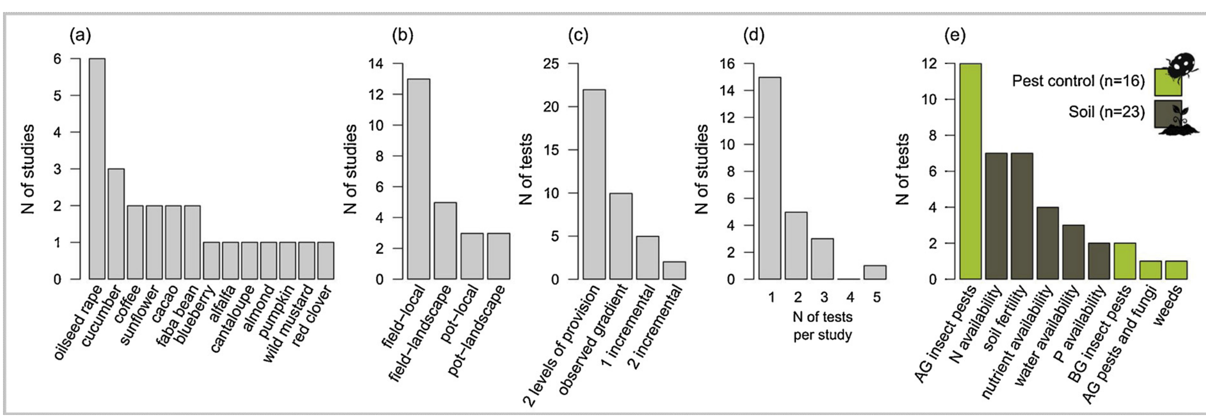

Fig. 2. The number of studies and tests grouped by (a) crop species; (b) type of experiment: field or pot, experiments performed in open field or with pots; local or landscape, experiments performed in one location or in multiple locations selected along a landscape gradient; (c) type of manipulation: 2 levels, observed gradient, one factor manipulated with more than 2 levels or both pollination and concomitant factor manipulated with more than 2 levels; (d) number of tests per study; (e) the concomitant factors investigated: water availability has been included in the "soil" category and weeds classified as pests. AG– Aboveground; BG – Belowground. Based on 39 tests from 24 studies (Tables 1 and S2). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

The literature search resulted in 24 peer-reviewed studies for a total of 39 individual statistical tests of interactions (Tables 1 and S2). All the studies were published since 2004 and 80% was published since 2013. Studies examined responses of 13 crop species (Fig. 2a), testing interactions both at the local and the landscape scale (16 and 8 studies, respectively) and under both field and pot conditions (18 and 6 studies, respectively; Fig. 2b). Eleven studies were performed in Europe, 6 in North America, 3 in South/Southeast Asia, 2 in Africa, 1 in Oceania and

1 in South America (Table S2). Most studies experimentally manipulated the levels of ES provision or management factors (ten were observational; Fig. 2c) and explored the interaction between pollination and one concomitant factor at a time (i.e. two-way interactions; Fig. 2d). The concomitant factors explored can be grouped in two broad categories: soil factors (hereafter labelled as soil) and pest control (23 and 16 tests, respectively; Fig. 2e). The interactions between pollination and aboveground pest regulation, nitrogen (N) availability or soil fertility were the most frequently investigated, comprising 26 out of 39 tests. The factors were generally manipulated using categories with high (e.g. full insect pollination, standard soil fertility, no pests) *vs.* no or low provision level (e.g. pollinator exclusion, low soil fertility, high pest incidence). In two studies, the variation in pollination benefits was investigated along a continuous gradient, from low to high levels of fertilizer application (Tamburini et al., 2017; Garratt et al., 2018). Hence, tests of potential non-linear effects are largely under-represented in the literature.

General trends regarding the type of interactions occurring between pollination and other factors were drawn on the basis of 25 tests from 19 independent studies. About seventy percent of the tests reported significant interactions between pollination and the concomitant factor influencing yield (68%, Fig. 3). Pollination and concomitant factors most frequently acted synergistically, with pollination benefits maximized at high provision level of the second factor considered (59% of the significant interactions). Twenty per cent of the tests displayed compensatory effects of pollination and, in one case, pollination benefits were maximized at the intermediate level of the gradient. Pollination and pest control always had interacting effects, whereas nearly half of the interactions between pollination and soil factors were not significant.

3.1. Soil: nutrient and water availability

We found high availability of both nutrients and water to increase

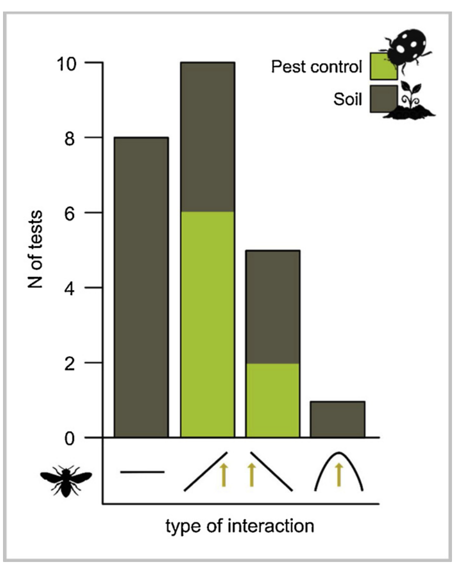

Fig. 3. Number of tests of interactions between pollination and soil factors (brown) and pest control (green). Tests are grouped by the type of interaction found as displayed in Fig. 1. Pollination benefits to crop production were found to be additive (independent from the provisioning level of a concomitant factor involved in crop production), maximized at high, low or intermediate provisioning level of a concomitant factor (from left to right, respectively). Based on a subset of 25 tests from 19 studies (Table 1; one test of a significant interaction between pollination and soil fertility was not included because the direction of interaction was not described, Bartomeus et al., 2015) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

pollination benefits to crop production in several crops (Klein et al., 2015; Tamburini et al., 2016a; Al-Kahtani et al., 2017; Garratt et al., 2018; Fig. 3). Shortages in these resources could have limited the proportion of fertilized ovules that developed into fruits or seed, ultimately reducing the potential benefits of pollination. For oilseed rape, cacao and faba beans grown under field conditions, pollination benefits tended to decrease with increasing nutrient availability, i.e. under higher nutrient availability plants compensated for the lack of pollinators by developing a larger number of fruits and seeds (Marini et al., 2015; Forbes and Northfield, 2017; Ramos et al., 2018). No such interactions were instead found between pollination and water availability in coffee, nor between pollination and nutrient availability or soil fertility in coffee, cucumber, faba beans grown in pots and oilseed rape (Boreux et al., 2013; Bartomeus et al., 2015; Motzke et al., 2015; Van Gils et al., 2016). Only in one case pollination benefits were found to be maximized at intermediate levels of nutrient availability (Tamburini et al., 2017). Interestingly, this was the only case where both pollination and soil factor were manipulated across a continuous gradient at levels higher than optimal. Soil effect on pollination benefits to yield was hence mixed, with only 53% of the tests reporting significant interactions. The lack of clear general patterns indicates that the influence of nutrients and water availability on pollination benefits might be highly context dependent. Crop species-specific characteristics might play an important role in shaping these interactions.

3.2. Pest control: insects, diseases and weeds

Pests and diseases can dramatically influence yield in flowering crops and were found to affect pollination benefits in all the studies (Fig. 3). Both natural and chemical control of pests were shown to generally increase pollination benefits in several crops (6 out of 8 tests). Insects attacking reproductive structures cancelled pollination benefits in oilseed rape, wild mustard and red clover because of their direct damages to flowering structures, reducing the number of viable flowers, fruits or pollinator visits (Sutter and Albrecht, 2016; Van Gils et al., 2016; Lundin et al., 2013; Grass et al., 2018). Similar patterns were observed in blueberry not treated with pesticides: the combined action of fungal diseases (*M. vaccinii-corymbosi*) and insect pests affected the crop's capacity to produce flowers and to sustain fruit ripening, limiting pollination benefits on fruit set but not on yield (Melathopoulos et al., 2014). In one case, high levels of pest abundance led to increased pollination benefits and yield in oilseed rape, suggesting notable compensatory (growth) response of attacked crop stands (Bartomeus et al., 2015). Moreover, enhanced pollination compensated for the negative effects of leaf herbivory on cantaloupe yield (Strauss and Murch, 2004). Weeds can greatly affect crop production through competition for resources among plants. Impact of weeds on pollination benefit was explored in only one study where pollination and weed control synergistically enhanced yield in cucumber (Motzke et al., 2015).

4. Potential mechanisms driving interactions between pollination and concomitant factors

Pollination and its contribution to seed formation is connected to plant physiological processes (Knight et al., 2005). We therefore suggest to explore how concomitant ES, crop management and crop life history traits alter resource availability for reproduction and resource allocation strategies in order to better understand the mechanisms driving the variability of pollination benefits in crop production.

4.1. Resources

The degree of pollen limitation is generally expected to increase at higher levels of resource availability (Fig. 1b) when the number of fertilized (pollinated) ovules is the limiting factor in terms of seed production (Haig and Westoby, 1988; Burd, 2008). However, when

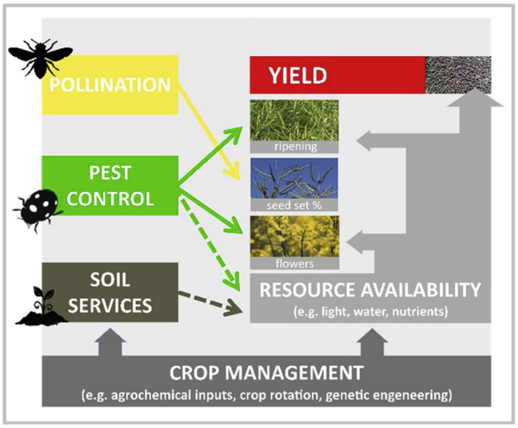

Fig. 4. Overview of the factors influencing the yield formation process in flowering crops. Pest control and soil factors affect the amount of resources the plant can allocate to reproduction or directly influence reproductive structures. Crop management influences resource availability, the provision level of several services and it can affect yield formation processes (e.g. genetic engineering). Solid line, direct effects on reproduction; dotted line, indirect effect on reproduction through altered resource availability.

resources are limited, the number of pollinated ovules becomes less important than the maximum number of seeds that can actually develop: resource availability becomes the major limiting factor. These predictions are supported by our review of literature, as the majority of significant interactions between pollination and the concomitant factor expected to increase yield were synergistic. Nevertheless, we also found non-synergistic interactions, with pollination benefits maximized at low or intermediate levels of the concomitant factor. The actual level of resources available for crop reproduction is difficult to compare among studies when only two levels are tested. It is therefore possible that different types of interactions are simply the results of the use of a small part of the potential resource gradient.

Concomitant services and management practices can affect the resource budget for reproduction in a number of ways (Fig. 4). Low levels of soil resources or pest control might limit or erode this resource budget, decreasing the expected pollination contribution to yield. Soil fertility and structure for example directly influence the availability of nutrients and water to plants. Soil biota such as growth-promoting rhizobacteria, earthworms and mycorrhizal or endophytic fungi can positively affect crop yield, potentially improving pollination benefits through increased resource acquisition capacity and disease resistance (Orrell and Bennett, 2013). The resource budget for reproduction in plants can also be limited by pests because of limited access to those resources in the surrounding environment (e.g. from weed competition), direct removal (herbivory) or reallocation of resources to defence mechanisms. For example, in response to herbivory, plants can either produce chemical and morphological defence traits to deter herbivores, or mobilize stored reserves for regrowth and reproduction after biomass loss (Karban and Myers, 1989). In both cases, this may result in lowered resource availability for reproduction, potentially affecting yield (Lucas–Barbosa, 2016). However, the frequently observed non-significant interaction between pollination and resource treatments could reflect the plasticity of plant responses to resource imbalance in their investment to reproduction (Campbell and Halama, 1993; Knight et al., 2005; Wesselingh, 2007).

4.2. *Crop life-history traits*

Specific life history traits can be important in understanding the response to resource and pollen variability among crop species. We hypothesize three life-history traits to be particularly important in shaping impacts of ES and management on pollination benefits: pollination dependency, flowering strategy, and life span. Given the limited number of analyses, we pooled together different types of interactions.

4.2.1. *Pollination dependency*

Pollination dependency is a genetically based mechanism which controls mating by imposing a physiological barrier for self-fertilization, evolved to encourage outbreeding in flowering plants. Basic information on the level of pollinator dependence is, however, incomplete for many crops (but see Bartomeus et al., 2014) and might differ among cultivars (e.g. Marini et al., 2015). Crop species characterized by a low dependency on animal pollination are expected to be less subjected to interactive effects of pollen and resource variability because pollinator visits influence less strongly reproductive outputs in the first place. Our review supports this hypothesis (Fig. 5a): significant interactions were more frequent when the crop species was highly dependent on pollination (89% significant interactions) than when the crop was more self-compatible (56%; pollination dependency based on

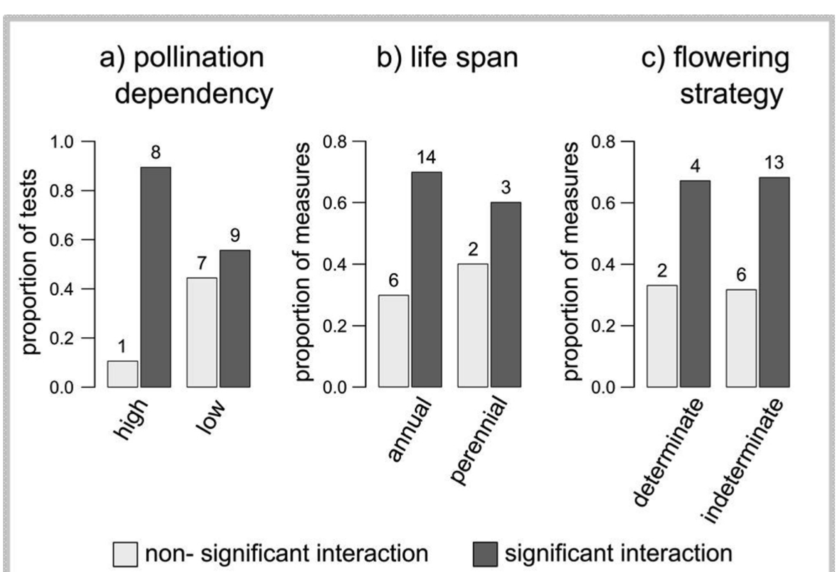

Fig. 5. Effects of crop life history traits on the significance of the interactions between pollination and concomitant factors influencing yield. Numbers above the bars refer to the number of tests belonging to each category. Based on a subset of 25 tests from 19 studies (Table 1).

Klein et al., 2007). Significant interactions were more frequently synergistic (6 out of 8, 4 out of 9, respectively). Even if not conclusive, this trend indicates that the higher the pollination dependency of a crop, the higher is the probability of concomitant factor to affect pollination benefits.

4.2.2. Life span

Resource accumulation and storage is essential for all plants as it buffers asynchronies between resource supply and the resource demands. Perennial long-lived species (mainly tree crops in agriculture) have a higher capability of storing resources in roots and stems compared with annuals that, instead, depend more on the resources available in the surrounding environment at a given time. The mobilization of stored resources increases the ability of long-lived plants to produce more flowers and/or increase seed weight, potentially compensating for the yield loss induced by pollen limitation. Perennial crops should thereby be better able to cope with both pollen and resource limitation through reallocation of reserves to reproduction. The studies we found partially supported this hypothesis, as interactions were more frequently found for annual crops (70% interactions, 57% of which synergistic) than for perennial crops (60%, of which2 out of 3 synergistic; Fig. 5b). Nevertheless, perennial crops were less represented than annuals (5 tests out of 25). More studies will be needed to clarify if perennial crops are less subject to interactive processes between pollen and resource availability.

4.2.3. Determinate and indeterminate flowering strategy

Some plants develop all their flower buds before the flowering season, without the opportunity to change the number of flowers later, i.e. flowering is determinate. Examples include trees such as apples, cherries, pears, and annual crops such as sunflower and red clover. In case of low levels of pollen deposition and thereby of fruit set, these crop species would not be able to adjust the number of flowers produced, but could redirect resources for seed provisioning, eventually increasing seed size. If the number of flowers is not fixed, i.e. flowering pattern is indeterminate, a plant can react to low pollen deposition and fruit set by investing into the production of new flowers. How well the plant compensates for the limited pollination through resource reallocation depends on the resource availability to the plant. Moreover, plants in resource-rich environment are generally more plastic in their allocation in response to environmental stresses than those living in resource-poor environments (Bloom et al., 1985; Wesselingh, 2007). Hence, we expected crop species with determinate flowering to score a higher proportion of significant interactions being less able to adapt to resource and pollen imbalances. However, we found little support for this hypothesis: crop species with both determinate and indeterminate flowering strategy displayed a similar proportion of significant interactions (67 and 68%, respectively; Fig. 5c). However, the determinate flowering strategy was less well represented (6 tests out of 25). Interestingly, we found compensation mechanisms (Fig. 1c) mainly for crops with indeterminate flowering, suggesting that these crop species are better able to compensate for pollen limitation at high levels of resource availability.

5. Methodological approaches to study interactions

Understanding of how complex combinations of ES and management factors might affect pollination benefits will require several complementary approaches. Below, we review the weaknesses and strengths of the methodological approaches that have been used.

5.1. Manipulative experiments

Single, isolated plants are expected to respond more strongly to resource manipulations than a crop stand (e.g. Tamburini et al., 2016a; Garratt et al., 2018). For example, competition in a crop stand could reduce the ability of a single plant to compensate for the lack of pollination. Similarly, plants grown in pots might respond more strongly compared with plants grown under field conditions because of limited access to soil resources. In some situations, however, pot experiments might represent the best solution for particular treatments (e.g. belowground herbivory) or to avoid variation in environmental conditions such as differences in soil fertility. We suggest therefore, whenever possible, to perform studies under realistic field conditions and use pots as a complementary approach.

The majority of the studies directly manipulated ES provision or management by establishing only two – often extreme – experimental levels. Pollination benefits have been evaluated predominantly by measuring yield losses due to a complete lack of pollinators, and only a few explored their incremental contribution. However, this approach does not account for the variation in pollinator density and diversity occurring in nature. Pollination is expected to decrease in response to human disturbance rather than be completely nullified. As a next step, we suggest to explore the incremental contribution of different services or management factors as a complementary approach to improve predictions of impacts of changing environmental conditions on crop production (Garibaldi et al., 2016; Van Gils et al., 2016; Tamburini et al., 2017).

5.2. Observational studies

Ten studies explored interactions between pollination and concomitant factors by correlating different indicators such as pollinator and fertilization or pest abundance in the field (e.g. Boreux et al., 2013; Bartomeus et al., 2015; Perrot et al., 2018; Ramos et al., 2018). This approach is complementary to manipulative experiments as it takes into account natural complexity, but has the disadvantage of uncertainty in the cause-effect relationships between variables. For instance, two correlated variables might respond to a common driver rather than influencing each other. We suggest to use the experimental manipulation as first step to assess whether interactions do occur, and to perform observational studies, preferably along orthogonal management or environmental gradients, to validate the relevance of these processes at the landscape scale.

6. Study limitation and research gaps

Our review explores a recently emerged field of applied ecological research. The main limitation of our study is consequently the limited number of studies available on the topic. Moreover, the selected studies were performed in different cropping systems and with different experimental approaches, which is reflected in the variability of interactions observed. Nevertheless, the patterns emerged clearly show the importance of considering context dependency when managing pollination services and the need for future research. Our review in fact highlighted several knowledge gaps: worldwide important crops such as tomatoes and apples have never been tested for potential interactions, coffee and cacao only with few studies. The effects of pathogens and belowground pests in general are highly underrepresented compared to other categories. Interactions between pollination and water availability needs to be further investigated, especially considering the higher occurrence of extreme weather events expected under current climate change scenarios. Moreover, research is needed on how multiple ES and management simultaneously affect yield (e.g. Tamburini et al., 2016b; Finney and Kaye, 2017). Finally, we need a better understanding of the role played by crop traits in shaping the effects of concomitant services and management on pollination contribution to yield.

7. Conclusions: implications for management

We found interactions between pollination and other factors influencing yield to be prevalent across several crops and mostly displaying positive-synergistic relationships. Soil properties and crop pests are expected to affect the contribution of pollination to yield by altering the amount of resources a plant can allocate to reproduction, independently of the amount of pollen provided. However, strategies to counteract pollination deficiency in crops have mainly consisted of interventions to improve semi-natural habitats around the fields (e.g., Carvalheiro et al., 2011; Holzschuh et al., 2012; Korpela et al., 2013; Scheper et al., 2013; Andersson et al., 2014; Blaauw and Isaacs, 2014). However, these strategies might fail in providing pollination benefits in landscapes characterized by poor soil resources or ineffective pest control. Agricultural intensification together with poor soil management have led to widespread degradation of soils worldwide and, despite the intense use of chemical pesticides, estimated crop losses to pests have increased globally (e.g. Powlson et al., 2011; Tilman et al., 2011). Our results stress the importance of considering all the services and management factors that potentially alter resource availability for crop reproduction when planning strategies to maximize crop pollination benefits in agroecosystems. Bommarco et al. (2013) hypothesized that limitations to yield production might be set by the lowest regulating or supporting service, even if other services could sustain higher levels of yield. It is possible that the provisioning level of some services or the availability of management-related resource sets a limit to the contribution level of the others. The results from our review suggest that interactions between pollination and soil factors or pest control influence several cropping systems, mostly by synergistic interactions.

We are now beginning to understand how the ES and management factors involved in crop production can be linked to plant physiological processes such as resource acquisition and allocation to growth, defence and reproduction. Deeper understanding of crop-pollinator interactions will benefit from focussing more on plant developmental and physiological traits and responses. Moreover, management interventions aiming at supporting pollination benefits and not only pollination provisioning need to be identified. Flower strips, for example, might increase pollination benefits because of the synergistic effects of enhanced pollinator and natural enemy communities, simultaneously supporting pollination and pest control services. Adding prairie strips to cropland has been shown to increase at the same time pollinator abundance, water availability, and soil and nutrient retention (Schulte et al., 2017). On the other hand, it is important to consider potential negative secondary effects of particular management practices. For example, soil management aiming at increasing soil organic matter might sustain more abundant pest populations (Tamburini et al., 2018); lower pest damage through pesticide application might increase the potential for pollination benefits, but might decrease pollinator abundance in real landscapes (Rundlöf et al., 2015).

A major future challenge will be to guarantee global food security and at the same time reduce the negative impacts of agricultural systems on the environment. Combining the knowledge from plant physiology and ecology with novel management practices could serve to maximize pollination benefits supporting crop production while reducing external inputs.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.04.022.

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