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Author

Tscharntke, T, Ocampo-Ariza, C, Kämper, W

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Opinion

Pollinator, pollen, and cultivar identity drive crop quality

Teja Tschamtké ^{1,*}, Carolina Ocampo-Ariza¹, and Wiebke Kämper^{1,*}

Animal pollination enhances a third of global food production, yet the roles of pollinator, pollen, and cultivar identity in shaping crop quality, such as nutritional, sensory, and marketing value, are underexplored. Crop quality often depends on pollinator movement patterns, which vary with cultivar selection and spatial arrangement, pollen donor identity, and landscape context. Transfer of the right pollen between cultivars may fail, as pollen is often not transported far, even by highly dispersive pollinators, reducing cross-pollination and crop quality. Both pollinator identity and complementary spatiotemporal activity of diverse pollinators can shape crop quality. Here, we argue that promoting crop quality needs better understanding of species-specific pollinator behaviour and cultivar distribution patterns, rather than only focusing on enhancing pollinator densities.

Pollinators promote crop quantity and quality

Animal pollination benefits 75% of the major crop species and 35% of food production globally [1,2]. The estimated economic value of animal pollination services is high, equalling US\$235–577 billion annually [3], even without considering current continuous increases in value caused by, (i) a rise in the area of pollinator-dependent crops [2], (ii) people getting richer [4], (iii) ecosystem services like pollination becoming scarcer [4], and (iv) the contribution of the high nutritional value of pollinated crops to human health globally. Crop plants that depend fully or partially on animal pollinators (e.g., many fruits, nuts, and legumes) contain more than 90% of vitamin C in our diet as well as nutritionally important carotenoids and antioxidants [5]. Bees improve the nutritional value of oilseed rape (*Brassica napus* L.) by increasing the amount of polyunsaturated fatty acids and higher oil content [6] and promote the oil content and fruit weight of avocado (*Persea americana* Mill.), enhancing marketability [7]. Crop pollination is a highly dynamic process as pollinators exhibit spatial and temporal changes in community composition [8–10]. Furthermore, different crops experience different pollinator communities. For example, broad beans (*Vicia faba* L.) are mainly visited by bumblebees, whereas oilseed rape receives visits from a diverse mixture of pollinators [11,12] (Figure 1). Trait matching between flower visitors and crop flowers has been identified as crucial for fruit set in a review [13]. The quantitative and qualitative evaluation of pollination services becomes even more complex, when the relation between the identity of the pollinator species, the identity of the deposited pollen, and the resulting fruit quality is considered. The focus on general patterns in crop–pollinator relationships typically neglects more sophisticated analyses of the combined and interactive effects of pollinator, pollen, and cultivar identity. Moreover, the widespread focus on crop yield usually leaves possible effects on fruit quality unexplored.

For pollination success, enough pollen needs to be deposited on the female organs of a plant's flower to guarantee fertilisation [14,15]. Heterospecific pollen transfer negatively affects pollination success [16], but even in the case of conspecific pollen, the genotype of the deposited pollen

Highlights

Crop quality is driven by interactions between pollinator species, pollen genotype, and plant cultivar, but this topic is poorly explored.

The genetic identity of transferred pollen (parentage) and the selection and spatial arrangement of cultivars within plantations determine pollination success and quality.

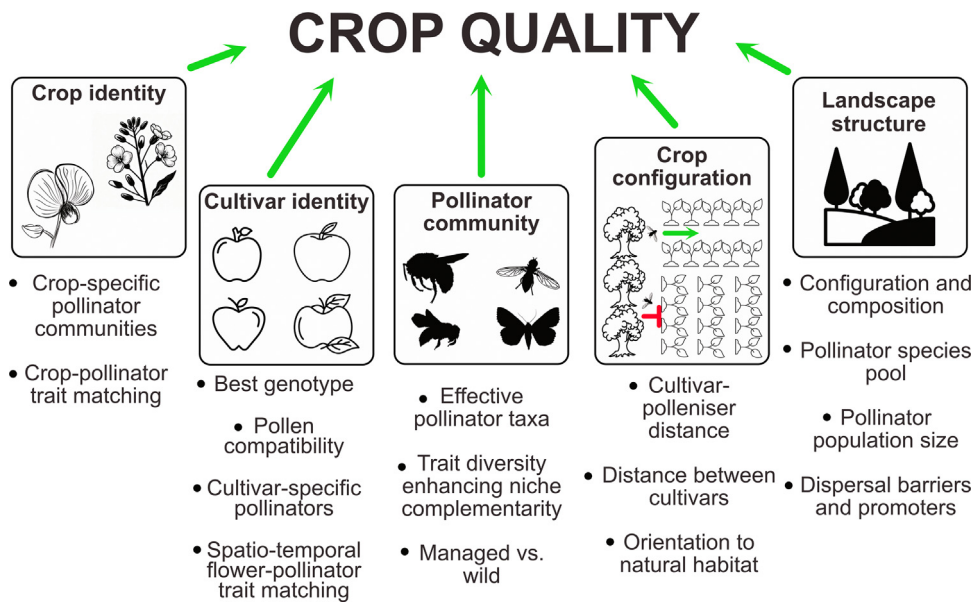
Pollinator species differ in their foraging patterns in crop plantations and may transfer unsuitable pollen genotypes, limiting production and crop quality.

Pollinator identity shapes pollination success in several pollination syndromes, while complementary activity of different species in space (spatial distribution of flowers) and time (seasonal changes, day vs. night pollination) can also increase crop quality.

Smart cropland designs and adjacent pollinator-friendly landscapes may boost crop quality by promoting pollinators' pollen transfer among desired cultivars.

¹Functional Agrobiodiversity and Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

*Correspondence: ttschar@gwdg.de (T. Tschamtké) and wiebke.kaemper@uni-goettingen.de (W. Kämper).



Trends in Plant Science

Figure 1. Five main drivers of crop quality (i.e., the sensory, nutritional, and marketing value of fruits). Crop identity defines pollination traits and the role of pollinator species or assemblages. Cultivar identity can have a large effect on self- and cross-compatibility, influencing the size and quality of fruits. Pollinator communities may be diverse, enhancing crop quality through niche complementarity, while major or even unique species can dominate. Crop configuration considers pollinator movement in plantations, including the distance to suitable cultivars and the crop row orientation towards adjacent natural habitat. Landscape structure determines the pollinator species pool and pollinator density and shapes dispersal opportunities. Icons from Paul Spitzner©, www.PhyloPic.org, and www.thenounproject.org.

often determines pollination success and fruit quality. The genotype of the deposited pollen may depend on the pollinator species, particularly, when movement patterns are species specific. Hence, pollinator identity can influence fruit quality, as the source of the pollen (i.e., the pollen parentage) is well known to affect this trait, a phenomenon called xenia. Several studies show that pollinator species exhibit preferences for certain crop cultivars [17–20]. For example, in apple (*Malus domestica* Borkh.), cultivars differ greatly in the community composition of flower-visiting pollinators [21]. Pollinator identity and community composition may also greatly vary spatially and temporally [10] (Figure 1).

Only a few papers address the economic value of nutritional differences mediated by pollination [21,22]. Phytohormone responses to pollination and biochemical pathways with consequences for fruit quality are also little studied [23]. To get the right pollen on a flower of the right cultivar, hand pollination can be a straightforward solution in some crops [24]. Deposition of effective cross-pollen, avoidance of heterospecific pollen or pollen of inferior quality can be controlled and supported by hand pollination, but this task is extremely laborious and labour costs are high [24].

Fruit quality is shaped by pollinator–cultivar interactions

Fruit quality of roughly a quarter (23%) of crop species important to the human diet depends on animal pollination. However, crop quality measures are not standardised [25]. Organoleptic or sensory characteristics, established by trained testers, have strong subjective components and are often driven by consumers’ expectations and purchase preferences [26]. Nutritional quality could also be used to evaluate crop quality, as nutrient-dense food can help in combating human health

issues [5,27]. Last but not least, marketing advantages, such as fruit size, colour, shape, firmness, and shelf life, represent commercially important quality traits [22,28]. Recently, Gazzea *et al.* [25] reviewed the important role of animal pollination in multiple crop quality traits, but how pollination and pollinators shape the quality of different varieties or cultivars is still little explored [15,22,29].

One example where the response diversity of cultivars to pollination has been analysed is strawberry (*Fragaria × ananassa* Duch.). Generally, bee-pollinated strawberry fruits have higher quality than wind- or self-pollinated fruits. They are heavier, have less malformations, increased redness, and reduced sugar:acid ratios, and are firmer, which improves shelf life; roughly 65% of wind-pollinated, but only 20% of bee pollinated, fruits show deformations [22,30] (Figure 2). However, these main effects do not consider the high variability among different cultivars. Shelf life, red-colour intensity, sugar: acid ratio, and fruit mass exhibit great, partly contrasting differences, contingent on the strawberry cultivar. For example, the shelf life of fruits from the self-pollinated Darselect variety is more than triple that of bee-pollinated Symphony fruits; red-colour intensity decreases with wind or self-pollination in Yamaska, but not in Symphony. Based on fruit quality measures, the commercial value of the cultivars Korona and Yamaska benefits substantially from bee pollination, but less so in Darselect and Symphony. Interestingly, electroantennographic

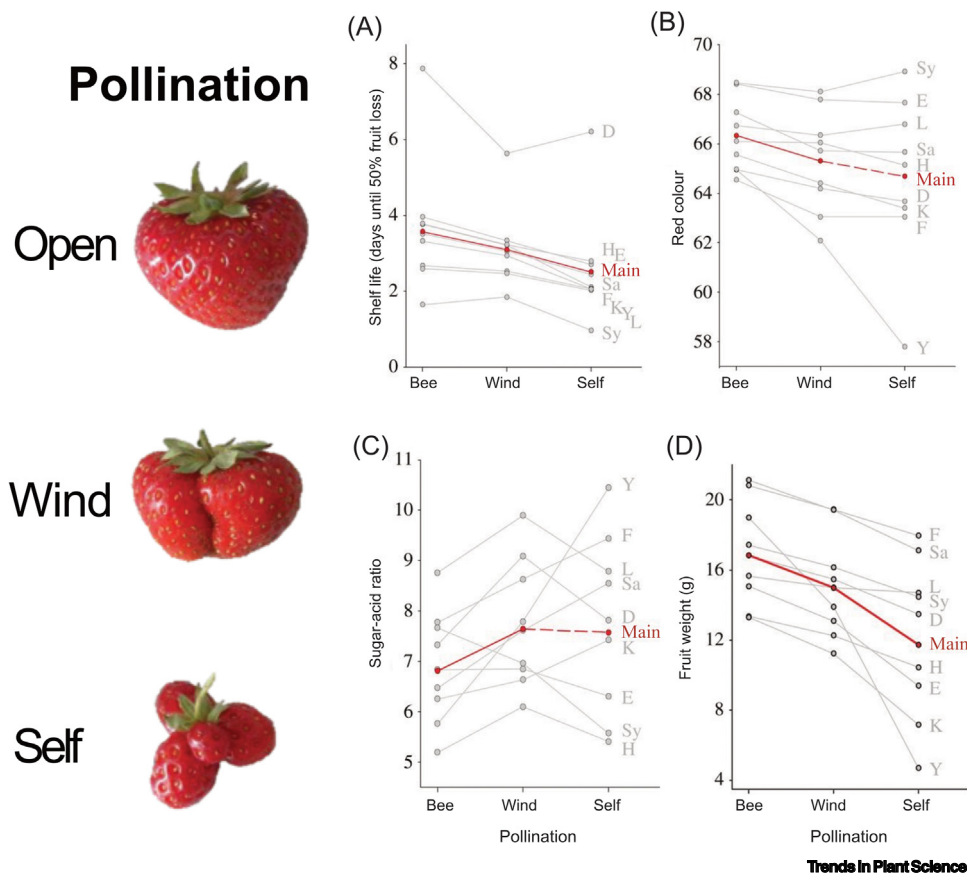


Figure 2. Fruit quality of strawberry cultivars in relation to bee, wind, and self-pollination. (A) Shelf life (in days until 50% fruit loss) is based on firmness values, (B) red-colour intensity, (C) sugar:acid ratios, and (D) fruit mass (g). Flower visitation by 98.5% bees, with 34% honeybees and 65% wild bees. Unbroken red lines show the main effect, the black lines the effect for each cultivar. Abbreviations of the commercial strawberry cultivars: D, Darselect; E, Elsanta; F, Florence. Main, main effect; H, Honeoye; K, Korona; L, Lambada; Sa, Salsa; Sy, Symphony; Y, Yamaska. Graphics from [22,30].

recordings with females of the solitary bee *Osmia bicornis* reveal that the cultivar Sonata emits more flower volatiles than Honeoye and Darselect, which leads to higher levels of the bees' flower visitation [31]. The high genetic variability among strawberry cultivars illustrates the importance of agronomic selection of commercially important traits, with its usually unintended consequences for attracting pollinators and their pollination success.

In cacao (*Theobroma cacao* L.), native cultivars also differ in pollen suitability for fruit set and size [15,32], while the cultural heritage of particular cultivars and corresponding fruit shapes are an important national and social good [32]. Increased floral visitation of highland coffee (*Coffea arabica* L.) leads to larger (supremo-type) coffee beans, which are regarded as of superior quality [29,33], but cultivar differences are not explored.

Cross-pollination typically increases crop quality compared with self-pollination. Outbreeding depression, known from wild plant populations [34], leading to lower fruit quality or yield has not been reported in crops. Apple, olive (*Olea europaea* L.), and almond [*Prunus dulcis* (Mill.) D.A. Webb] cultivars differ in sensitivity to self-pollination and poor pollen quality, and dependency on cross-pollination, respectively [35–37]. Wild bee pollination leads to larger strawberries than honeybee pollination, even when the same amount of pollen is deposited, possibly due to more cross-pollen being transferred by wild pollinators than honeybees [38].

Pollen parentage effects are strongest in plants that benefit from cross-pollination, which is pollination between plants of differing genetic composition, such as different cultivars or varieties in clonally propagated crops [14]. For example, the yield and quality of avocado [39], macadamia (*Macadamia integrifolia* Maiden & Betche) [40], and mango (*Mangifera indica* L.) [41] are known to vary according to pollen parentage and cultivar identity. Farmers are aware of the importance of cultivar identity and cross-pollination for many crops and, in some crops, plan the layout of orchards or fields correspondingly [42], but these decisions are complex and often made with only limited information. Later, we provide more insight on the complexity of the genetic landscape of crop–pollinator interaction influencing crop quality.

Pollinator movement patterns and pollination success

Which cultivar or variety provides the most successful pollen may also depend on the pollinator species visiting, and transferring, pollen to other flowers. However, this link appears to be little explored and is influenced by the design of the local cropland and the surrounding landscape. Pollinators are attracted by plant features such as volatile blends [31,43] as well as nectar quantity and quality [17], greatly differing among crop varieties. We often do not understand what proportions of the crop result from self- or cross-pollination, how cross-pollination affects crop quality, or how far cross-pollen is transported. Pollinator identity can affect pollination success because of specific movement patterns during foraging. Movement and behaviour of flower visitor taxa may affect the selection of the genotype of the pollen that is transported and deposited onto the stigmas of crop flowers. In cropping systems, flower visitors usually do not need to travel far or visit multiple plant individuals, as floral resources are abundant. Visiting only one or a few plant individuals during a single foraging trip is likely to limit the number of genotypes carried as pollen, especially in mass-flowering crops. Cross-pollinated crops require the presence of nearby well-selected genotypes within a plantation to maximise positive parentage effects. Bees with cross-pollen often travel only short distances in apple, avocado, chestnut (*Castanea sativa* Mill.), oilseed rape, mango, and macadamia crops [44–47].

Macadamia nut production depends on cross-pollination [40,48]. Macadamia trees are typically planted in single-cultivar rows or single-cultivar blocks, so that across-orchard transport is

needed to transfer cross pollen, hereby ensuring an effective pollination service that maximises nut size and nutritional quality such as the oil content [40,48]. The number of harvested nuts decreases already at 24 m from a cross-pollen source, suggesting that different cultivars should be interplanted more closely in macadamia orchards [40]. Hence, pollinator visitation, fruit quantity, and fruit quality can be much enhanced by orchard design. For example, apple cultivars are often self-incompatible and require cross-pollination from a suitable and nearby ‘polleniser’ cultivar, promoting fruit set and fruit quality; hence, orchard designs closely intermixing polleniser and production trees assure pollination across the orchard [42,49].

Honeybees, in particular, prefer to forage along rather than across rows in apple and almond orchards [44,50], which may make honeybees ineffective pollinators, when the cropping system depends on cross-pollen transfer across rows [40]. On the contrary, some fly species perform more erratic movements [51], increasing the chance of coming in contact with the pollen of multiple genotypes planted in different rows. Differences in the pollen genotypes carried by different flower visitor taxa could explain why pollination limited to honeybees can lead to reduced cross-pollination and low crop quality compared with pollination by a diverse flower visitor community, given the same amount of pollen deposited per visited flower [38,52,53]. Open insect pollination improves apple quality, looking at their size, mass, and classification for market, compared with hand pollination [21]. As foraging patterns of different flower visitor taxa are poorly described, it is mostly unclear whether behavioural differences determine the genotypes and the number of genotypes carried by different flower visitor taxa, and the cascading effects that this could have on yield and crop quality.

Landscape context of pollination communities and pollination success

The composition and configuration of the surrounding landscape determines the species pool and population size of pollinator populations that may colonise cropland [54–56], which consequently may affect not only crop yield but also crop quality. However, effects of landscape context on cultivar–pollinator interactions influencing fruit quality are almost unknown [57]. Complex landscapes allow more and a higher diversity of flower visitors to enter cropland. For example, sweet cherry orchards benefit from surrounding seminatural habitat, with more than doubled yields due to many wild bees rather than honeybees [58]. Landscapes comprising small fields with long edges can support five times more wild bees and higher pollination success than landscapes with large fields [59]. Simplified landscapes (e.g., dominated by maize) provide only low pollen diversity, thereby largely reducing bumblebee colony growth [60]. In a field experiment with potted strawberries (cultivar Korona), berry mass (i.e., fruit quality) was highest near hedgerows connected to forest and reduced by 29% at isolated hedgerows and 32% on grassy margins [61]. Plants placed at forest-connected hedgerows produced more high-quality strawberries, with 90% classified as ‘marketable’ compared with only 75% at isolated hedgerows and 48% on grassy margins. A total of 41% of strawberries from self-pollinated control plants were classified as marketable [61]. Macadamia nut set increases threefold in case of perpendicular orientation of the planted macadamia rows towards the surrounding seminatural habitats compared with row orientation parallel to the surrounding seminatural habitats [62]. Not only orchard configuration but also landscape configuration may provide barriers for pollinator dispersal, such as large cereal fields or high hedges, as well as promoters such as high edge density and grassy strips or living fences [59,63,64].

Diversity of pollinator communities

Pollinator identity and species-specific pollinator movement drive pollination success in several specialised pollination syndromes [65], but complementary activity of different species in space (spatial distribution of flowers, habitat characteristics) and time (seasonal changes, day–night)

can also increase crop quality, thereby emphasising the importance of conserving a diverse pollinator community [10,66]. Diverse pollinator communities may enhance crop pollination by spatially and temporally changing sets of functional traits [8,67–70], but effects on fruit quality and the importance of cultivar differences are not documented. Crops that flower during an extended period may benefit from a turnover of pollinator species across days or months [10], with different management required for early-season and late-season communities [71] and under climate change [72]. In strawberries, pollinator taxa visiting flowers change throughout the season and respond differently to changing weather, where flies visit flowers in poor weather and at the end of the flowering season when other pollinators are scarce, thereby providing a unique functional contribution [73]. Complementary pollination by a species-rich pollinator community is also known from pumpkin (*Cucurbita moschata* Duch. ex Poir.), with pollinator species differing in flower height preference, daily time of flower visitation, and within-flower behaviour, which can result in enhanced fruit quality such as fruit size [8]. Pollination success in highland coffee increases with higher diversity, not abundance, of flower-visiting bees [67], while bee concentration or dilution on branches and shrubs depends on the spatial scale considered [74]. Bee-pollinated coffee has not only 9% higher fruit set but also a 2% enhancement in aroma and body compared with self-pollinated plants, as assessed by professional cuppers [75]. In the case of the bat-pollinated crop pitahaya [*Stenocereus queretaroensis* (F.A.C. Weber) Buxbaum] in Mexico, exclusion of the major bat species leads to reduced fruit quality, with fruit being lighter and less sweet [76]. Pollinators in raspberry (*Rubus idaeus* L.) contribute twice as much in the early- than in the late-flowering period, and the early-flowering period is dominated by a diverse group of native pollinators, whereas the late-flowering period is dominated by managed honeybees and bumblebees [77]. Natural flowering longan trees (*Dimocarpus longan* Lour.) are most frequently visited by wild bees, whereas off-season flowering longan trees are most frequently visited by dipterans, leading to reduced yields at off-season flowering [78]. In strawberry, nocturnal pollination produces heavier fruits, thereby increasing fruit quality, compared with those pollinated during daytime only [79]. In general, the niche complementarity between day-active and night-active pollinators is little explored.

Concluding remarks and future perspectives

According to recent research, pollinator identity, pollen origin, and crop cultivar determine not only the yield of pollinator-dependent crops but also crop quality (Figure 1). We encourage future research to focus on the drivers of commercial success in pollinator-dependent crops, which can benefit consumer health when the nutritional composition of crops improves (see Outstanding questions). There is a need for smart crop designs considering the spatial arrangement of crop cultivars that attract pollinators, thereby improving crop yield and quality. We propose that future research on the role of pollinators for crop quality focuses on the following main aspects: (i) crop quality in terms of the nutritional value provided by enhanced animal pollination; (ii) the role of pollinator identity, community composition, and trait complementarity in pollinator communities; (iii) facilitation of cross-pollination considering crop cultivar and pollen identity; (iv) attractiveness of flowers and flower rewards in the genetic breeding of new cultivars to improve flower visitation and pollination success, which may benefit fruit quality and yield; (v) comparison of self-pollinating with cross-pollinating cultivars in terms of fruit quality and yield; (vi) designs of cropland and surrounding landscape promoting effective pollinator movement; and (vii) comprehensive social–ecological understanding of management needs for higher pollinator-driven crop quality [80] (see Outstanding questions).

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Outstanding questions

How do crop cultivar, pollen origin, and pollinator identity drive crop quality?

Which features of fruit quality (nutritional, sensory and marketing values) are most important and need more research?

How can optimised cropland design, spatial crop arrangement, and the surrounding landscape structure increase pollinator movement, pollination success, and fruit quality?

When is pollinator community composition more important than pollinator abundance for optimal fruit quality?

How do different pollinator taxa influence the transfer of optimal pollen genotypes?

How can crop plant breeding enhance pollinator visitation patterns and fruit quality?

Declaration of interests

No interests are declared.

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