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Courgette Production: Pollination Demand, Supply, and Value

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Abstract

Courgette (*Cucurbita pepo* L.) production in the United Kingdom is estimated to be worth £6.7 million. However, little is known about this crop's requirement for insect-mediated pollination (pollinator dependence) and if pollinator populations in a landscape are able to fulfil its pollination needs (pollination deficit). Consequently, pollination experiments were conducted over 2 yr to explore pollinator dependence and pollination deficit in field-grown courgette in the United Kingdom. Results showed that pollination increased yield by 39% and there was no evidence of pollination limitation on crop yield. This was evidenced by a surprisingly low pollination deficit (of just 3%) and no statistical difference in yield (length grown, circumference, and weight) between open- and hand-pollinated crops. Nonetheless, the high economic value of courgettes means that reducing even the small pollination deficit could still increase profit by ~£166/ha. Interestingly, 56% of fruit was able to reach marketable size and shape without any pollination. Understanding a crop's requirement for pollinators can aid growers in their decision-making about what varieties and sites should be used. In doing so, they may increase their agricultural resilience and further their economic advantage.

Key words: agroecology, cucurbit, economic valuation, fruit set, pollination dependence

As agriculture intensifies and habitat conversion to farmland continues, crop producers are frequently relying on managed pollinator species to fulfil their pollination needs (Mader et al. 2010). Increasing the abundance of species such as *Apis mellifera* L. can interrupt the damaging cycle of lower yields from a reduced diversity and abundance of wild pollinators, often caused by losses in (semi) natural habitat (Garibaldi et al. 2011). This is a common practice for growers of Cucurbitaceae (cucurbits or gourds; Free 1993), a large and genetically diverse plant family which are thought to have an "essential" requirement for insect-mediated pollination (Klein et al. 2007). In these cucurbit-growing areas, an increase in the supply of pollinators is advocated in almost all situations, regardless of surrounding landscape (Nerson 2007). However, there is concern that pollination services provided by managed and wild bees are still not enough to fulfil requirements for crop production (Schulp et al. 2014).

Consequently, many studies have attempted to quantify pollination deficit: the difference between current and optimum levels of pollination. Experimentally increasing the abundance of pollinators has been shown to increase yield of summer squash (Nerson 2007, Artz and Nault 2011), melon (Kouonon et al. 2009, Nerson 2009), and cucumber (Nerson 2009). Likewise, areas with a high diversity of bee species may also benefit from increased yield, as evidenced with pumpkin (Hoehn et al. 2008). This positive relationship between pollinator visitation and yield means that fruit set is directly dependent on pollinators and the ecosystems which support their populations. Therefore, results are highly dependent on the spatial and temporal context of the landscape surrounding each crop field.

Although these positive relationships demonstrate how a crop can benefit from insect pollination, they do not quantify a crop's requirement for insect-mediated pollination or "pollinator dependence." This is quantified by comparing fruit set from open- or hand-pollinated flowers with flowers which have had pollinators excluded. Excluding pollinators from some cucurbits has shown that fruit set is unable to occur (Hoehn et al. 2008) and that increased pollen loads can make fruit grow faster and larger (Stephenson et al. 1988, Artz and Nault 2011). However, the dependence of a crop species on pollinators is likely to vary between varieties (Knapp et al. 2016). For example, 22 out of the 33 summer squash varieties have been shown to set fruit without pollination (Robinson and Reiners 1999). Likewise, fruit set without pollination has also been observed in cucumber (Kushnereva 2008), watermelon (Sedgley et al. 1977), and additional varieties of summer squash (Kurtar 2003; Martínez et al. 2013, 2014). This type of fruit set, without pollination and therefore fertilization, is parthenocarpy. As evidenced by these accounts of cucurbit growing, understanding a crop's requirement for pollination and, in turn, how pollinators vary spatially and temporally in the landscape is essential to design and deliver optimum crop management. The economic value (EV) of pollination can be included in cost-benefit analyses to inform decision-making at a farm and policy level (Hanley et al. 2014). This is because valuation based on a crop's dependence for pollination will show the detrimental impact that a decline in pollinator populations may have, and valuation based on the pollination deficit will show the potential that increasing pollinator populations may have. Consequently, quantifying the economics of pollination is a fundamental way for growers to understand the implications that changes in pollinator populations may have on their yield and economic return. Despite the economic importance of many cucurbit species and their "dependence" on pollination, no studies have calculated the EV of pollination to cucurbit crops. In other high-value crops such as apple, economic valuations have shown that maximizing pollination could increase UK output by £5.7 million per year (Garratt et al. 2014).

In the United Kingdom, the nutritional value of cucurbits has increased their popularity and therefore, supermarket demand. To receive maximum profit from consumers, each supermarket has their own quality specifications which they require growers to achieve. Consequently, growers strive to produce perfectly formed fruit to ensure an adequate return for their efforts. This study focuses on the pollination dynamics of field-grown courgettes (*Cucurbita pepo* L.) as a model species for cucurbit crops, which, although grown over a relatively small area in the United Kingdom (mostly in Cornwall, Cambridgeshire, Worcestershire, and Sussex), are a high-value crop (~£8,000 per ha). Therefore, to understand whether the dynamics of pollination are affecting yield quality or quantity and to improve guidance to growers for obtaining productive and sustainable yields, we ask: 1) does pollination influence growth rate, quality, and quantity of fruits?, 2) are courgettes experiencing a pollination deficit, and does this increase with distance into a field?, and 3) what is the estimated EV of pollinators and their potential profitability to courgette production in the United Kingdom? These studies use the popular courgette variety 'Tosca,' a high-yielding, compact variety which is notably tolerant to powdery mildew, making it a popular choice for commercial production (P.E. Simmons and Son, personal communication 29 June 2016). Despite the potential for parthenocarpy, selectively-bred parthenocarpic courgette varieties are not currently grown at a commercial scale in the United Kingdom.

Materials and Methods

Sites

In 2015 and 2016, the pollination conditions of Courgette (var. Tosca) were manipulated in seven fields across Cornwall, United Kingdom. Tosca is a popular courgette variety in the United Kingdom, representing 37.9% of the market share (P.E. Simmons and Son, personal communication 1 April 2017). Courgettes were grown in outdoor (opposed to protected) conditions at a density of 13,585 plants per hectare. Each field (average field size of 5.2 ± 1.3 ha (S.E.)) was situated >2 km apart to ensure independent pollinator communities between fields (Vaissière 2010) and was conventionally managed with minimum chemical input other than fungicidal sprays (P.E. Simmons and Son, personal communication 29 June 2016). In 2015, 180 flowers were manipulated at two fields and in 2016, 300 flowers at five fields, totaling 480 flowers over the course of the study.

Pollination Treatments

As courgette is monecious, each female flower was assigned to one of the following treatments: hand pollination ($n = 60$), open pollination ($n = 60$), or no pollination ($n = 60$) in 2015 and hand pollination ($n = 100$), open pollination ($n = 100$), or no pollination ($n = 100$) in 2016. Hand-pollinated flowers were treated on the first day of anthesis around 8:00 a.m. with pollen from a male donor flower (from a neighboring plant) using a paint brush. Open-pollinated flowers were left to be pollinated naturally by insects visiting the fields. The no-pollination treatment was initiated the day before expected anthesis by securing PVC mesh bags with wire ties to female flowers. Bags had a mesh size of 0.2 mm, designed to be permeable to wind and rain yet exclude any pollinators. To the best of our knowledge, no commercially reared *Bombus terrestris* (L.) or *A. mellifera* colonies had been introduced within a 1-km radius of each farm. The level of pollinator dependence (the difference between open- or hand- and no pollination) can be interpreted as courgette's "demand" for pollen, whereas the pollination deficit (the difference between hand- and open-pollinated crops) indicates the "supply" of pollen in the landscape relative to maximal pollination.

All experimental flowers were individually identified with marker pen written on pieces of flagging tape, tied to the base of each fruit. To avoid the confounding effect of a plant investing in additional fruits from unmonitored pollination events, only one fruit per plant was studied (Stephenson et al. 1988, Avila-Sakar et al. 2001).

Quantity and Quality Measures

In 2015 and 2016, fruits were harvested 10 d postanthesis, weighed on scales, measured using a tape measure (length and circumference [circumference only in 2015]), and their sugar content (°Brix) recorded (only in 2016). °Brix is considered to be a simple and objective measure which can be used by growers to assess fruit quality, as sweetness is appreciated by consumers (Kleinhenz and Bumgarner 2012). °Brix was measured on a hand-held refractometer (Bellingham-Stanley, range 0–50%) by taking a homogenized value from three 1-cm^2 pieces of fruit (middle and either end).

Experimental fruits were classed as "aborted" if they did not meet minimum commercial standards (Ellis Luckhurst, personal communication 24th June 2015), i.e., they were <14 cm in length, 30 mm in width (at the mid-point), and over 5° in curvature, or showed any obvious signs of bacterial damage, such as blossom end rot. Therefore, fruit set (the ratio of marketable fruit compared with the total number of marked flowers per treatment) is also a measure of fruit quality. As fruit set was measured over 10 d, courgettes were generally larger than commercial standards. Because these experiments were conducted at a commercial farm, some fruits were accidentally removed by pickers. Consequently, final sample sizes were less than the number initiated and are not completely balanced between treatments (hand pollination, $n = 151$; open pollination, $n = 157$; no pollination, $n = 153$).

Effect of Pollination Over Time

In 2015, 180 of the experimental female flowers were measured at two fields (hand pollination [$n = 60$], open pollination [$n = 60$], and no pollination [$n = 60$]). Fruit length was measured daily from the first day of anthesis to 10 d postanthesis to explore the effect of pollination treatment on fruit length over time. All pollination treatments were conducted simultaneously within each field to minimize environmental variation between treatments.

Pollination With Distance Into a Crop

In 2016, a total of 100 experimental flowers were left to be pollinated naturally in five different fields at 0 m ($n = 50$) and 50 m ($n = 50$) into the crop from the field edge (10 flowers per field and location into the crop). In each field, the edge of the crop was a hedgerow. Therefore, 0 m into the crop was closer to seminatural habitat than 50 m in the crop. To observe bee visitation, three flowers (male and female; on the first day of anthesis) were randomly selected at each of these locations. This method was used (rather than sampling a unit area) because it was the best way of observing multiple flowers simultaneously. The majority of pollinator species were *A. mellifera* and *Bombus* species, so only these were identified to species level. *Bombus terrestris* and bees belonging to the *Bombus lucorum* (L.) complex were combined in a single group owing to difficulties in reliably distinguishing workers in the field (Murray et al. 2008). Bee visitors were recorded over two 15-min periods, at each field and location within the crop (0 m and 50 m from the edge), totaling four observational periods per field. Pollinator visitation rate was calculated as the number of visits per minute per flower summed across the two surveys for each of the two distances from the edge of the crop. All observations were done in sunny or mild weather conditions (>15 °C) with, at most, light wind, between 9:00 and 11:00 a.m.

Economic Value of Pollination

It is often assumed that a loss of pollinators will decrease the value of horticultural crops; however, yield is also dependent on variety, management practices, and environmental conditions (Bos et al. 2007, Boreux et al. 2013, Klein et al. 2014, Motzke et al. 2015). As these inputs improve, fruit quantity (fruits produced per plant over a season) and fruit quality (size and shape) will increase, improving the grower's economic advantage. Based on Melathopoulos et al. (2015), the EV of these combined factors (under open-pollination conditions) can be broadly estimated as:

$$EV = P \times Q \quad (1)$$

where EV (£/ha or £ for United Kingdom) is the total economic value per unit area, P is the price (£/kg), and Q is the quantity of crop grown (Kg/ha or Kg in United Kingdom). To estimate the EV of courgettes for the United Kingdom, and the proportion which depends on insect pollination, we have used national statistics and local data. P was calculated as the average weekly price (£/kg) of all courgette varieties (data were unavailable for individual varieties) from June to September, 2016 (Department for Environment Food and Rural Affairs 2016). Q was the average yield (kg/ha) of one courgette variety, Tosca, at the 2015 study site in Cornwall (P.E. Simmons and Son, personal communication 29th June 2016).

Using the pollination manipulations in this study, a coefficient of pollinator dependency (D) can be calculated as the fruit set as a result of open pollination (f_p) compared with pollinator exclusion (f_{pe}). D relates to pollinator dependency in particular conditions, whereas D_{max} is the maximum dependency of a crop on pollinators. D_{max} is calculated as the fruit set as a result of hand pollination (f_{pmax}) compared with pollinator exclusion (f_{pe}). These can be used to determine the extent to which fruit set would increase or decrease if pollination was improved or removed.

$$D(or\ D_{max}) = 1 - \frac{f_{pe}}{f_p\ (or\ f_{pmax})} \quad (2)$$

To calculate the EV of pollination ($IPEV$), i.e., the proportion of the crop's value that would be lost if all pollinators were removed, the total value of the crop (per hectare) is multiplied by D.

$$IPEV = EV \times D \quad (3)$$

On the other hand, if pollination was maximized (equivalent to hand pollination), then the maximum EV ($MaxEV$) of courgettes would be:

$$MaxEV = EV \times D_{max} \quad (4)$$

Subtracting $IPEV$ from $MaxEV$ reveals the pollination deficit ($PDef$) at a particular location. This is the potential profitability that pollinators could provide under maximal pollination conditions.

$$PDef = MaxEV - IPEV \quad (5)$$

(For further explanation of these equations, see Melathopoulos et al. (2015)).

EV, $IPEV$, $MaxEV$, and $PDef$ were all calculated for courgettes and then multiplied by the total area of courgette production (for all varieties) in the United Kingdom (Outdoor Cucurbit Growers Group, personal communication 22nd September 2016) to calculate values for UK production. Owing to a lack of data (in this study and the wider literature) on pollinator dependence and the area of different courgette varieties in the United Kingdom, figures are only based on one courgette variety (Tosca) for D and all varieties for P and Q.

Statistical Analysis

All analyses were performed in the R package lme4 (Bates et al. 2014). Error distributions were Gaussian unless otherwise stated, and residual plots were used to check for normality and heteroscedasticity. Post hoc Tukey tests were calculated using the multcomp package (Hothorn et al. 2008).

Pollination Treatment

The effect of pollination treatment (fixed effect) on fruit growth (length 10 d after anthesis; 2015 and 2016 data combined), weight (2015 and 2016 data combined), circumference (2015 data only), and °Brix (2016 data only) was tested, with field specified as a random effect.

Fruit set (the ratio of marketable fruit compared with the total number of marked flowers per treatment) was modelled using a GLM with a binomial error distribution, with field and pollination treatment as fixed effects.

Pollination with Distance Into the Crop

Fruit set (with a binomial error distribution), fruit growth (length after 10 d), weight, and °Brix under open-pollination conditions were assessed in relation to distance from the edge of the crop, pollinator visitation rate (visits per minute per flower, summed across the two surveys for each of the two distances from the edge of the crop) and their interaction as fixed effects and field was specified as a random effect. Pollinator visitation rate was assessed in relation to distance from the edge of the crop, with field specified as a random effect.

Results

Pollination Deficit and Pollinator Dependence

Fruit set of Tosca (in 2015 and 2016) significantly increased with hand- and open-pollination compared with no-pollination conditions; however, there was no significant difference between hand- and open-pollination (Table 1). Overall, fruit set was 98% for hand-pollinated flowers, 95% for open-pollinated flowers, and 56% under no-pollination conditions (Table 1). Over half of the experimental flowers subjected to the no-pollination treatment were able to set fruit to marketable size and weight (Table 1). However, fruit length, weight, and circumference (not °Brix) for nonpollinated flowers were significantly decreased compared with hand- and open- pollinated flowers (Table 1).

Table 1. Results from the LMMs and GLM on the effect of pollination treatment (hand pollination, open pollination, and no pollination) on field-grown courgette quality and quantity measures (mean ± SE)

Measure	Hand pollinated (mean ± SE (*n*))	Open pollinated (mean ± SE (*n*))	Pollinator exclusion (mean ± SE (*n*))	Tukey post hoc tests		*P*-value
				Contrast estimate ± SE	Test statistic (*z*-value)	
Fruit set (%)	98 ± 2.2 (151)	95 ± 2.9 (157)	56 ± 10.9 (153)	HP–NP: 2.71 ± 0.82	3.31	**0.003**
				OP–NP: 2.35 ± 0.77	3.07	**0.006**
				HP–OP: 0.35 ± 0.84	0.42	0.91
Fruit growth (length in cm after 10 d)	22.8 ± 0.5 (148)	22.0 ± 0.5 (149)	16.5 ± 0.8 (86)	HP–NP: 7.16 ± 0.68	10.56	**<0.0001**
				OP–NP: 6.26 ± 0.67	9.26	**<0.0001**
				HP–OP: 0.9 ± 0.57	1.56	0.26
Fruit weight (g)	829.9 ± 35.1 (148)	768.3 ± 33.2 (149)	520.1 ± 41.6 (86)	HP–NP: 362.6 ± 42.38	8.56	**<0.0001**
				OP–NP: 298.16 ±42.27	7.05	**<0.0001**
				HP–OP: 64.44 ± 35.8	1.8	0.17
Fruit circumference (cm)	17.4 ± 0.5 (60)	18.5 ± 0.7 (60)	15.0 ± 0.5 (60)	HP–NP: 7.43 ± 0.75	9.96	**<0.0001**
				OP–NP: 6.73 ± 0.74	0.94	**<0.0001**
				HP–OP: 0.7 ± 0.74	9.09	0.62
Brix	3.8 ± 0.04 (88)	3.8 ± 0.04 (89)	3.8 ± 0.08 (54)	HP–NP: 0.002 ± 0.08	0.03	1.0
				OP–NP: 0.07 ± 0.07	1.03	0.67
				HP–OP: 0.06 ± 0.08	0.86	0.56

N, the number of fruits analyzed.

Post hoc Tukey tests used to test for differences in pollination treatment are shown.

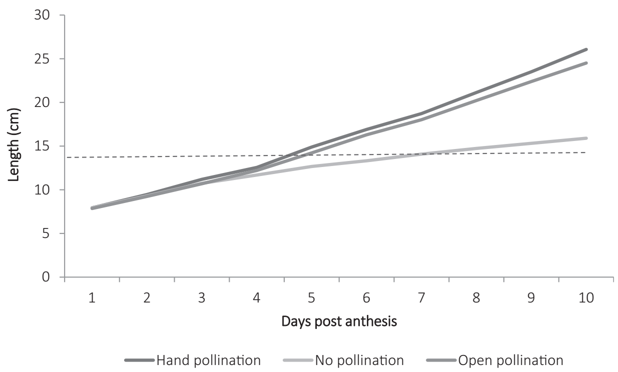

Fig. 1. Average daily length (y axis) of field-grown courgettes subject to pollination treatments (hand pollination, open pollination, and no pollination) over 10 d (x axis). The dashed lines show the minimum length required for commercial courgettes.

Effect of Pollination Over Time

Despite fruit length remaining similar for the first 4 d (just before fruits achieve a minimum marketable weight), nonpollinated fruits did not grow as long in length as open- and hand-pollinated fruits (Fig. 1).

Pollination With Distance Into a Crop

Distance from the edge of the crop had no effect on percentage fruit set, fruit growth, weight, and °Brix of open-pollinated plants (Table 2). Likewise, pollinator visitation rate (contrast estimate −4.68 ± 2.899 SE, $Z = -1.587$, $P = 0.11$) and the interaction between distance from the edge of the crop and pollinator visitation rate (contrast estimate 1.45 ± 4.33 SE, $Z = -0.336$, $P = 0.74$) did not influence fruit set. Overall, there was no change in pollinator visitation rate with distance from the edge of the crop (contrast estimate 0.04 ± 0.05 SE, $T = 0.72$, $P = 0.47$). However, *Bombus* spp. were more abundant at the edge of the crop, unlike *A. mellifera* which were more abundant within the crop (Fig. 2).

Economic Value of Pollinators

Courgettes are grown over 808 ha in the United Kingdom, which is not a large area compared with other crops, but each hectare of courgettes is worth over £8,000 to the grower in market value (Table 3). The current EV of courgettes in the United Kingdom is therefore estimated to be £6,694,632. Our pollination experiments demonstrate that the crops studied had a *D* of 0.41, i.e., 41% of fruit set was dependent on natural pollination (f_p compared with f_{pe}). This means that, if all UK crops are pollinated as well as they are in Cornwall, then pollinators contribute £2,744,735 to the total EV of courgettes in the United Kingdom (*IPEV*). The maximum dependency on pollinators under maximal pollination conditions (f_{pe} compared with f_{pmax}) was 0.43. Therefore, if the pollination deficit observed from our pollination experiments (although not significantly different from open pollination) is assumed to be similar across the United Kingdom, then there is scope to improve crop pollination by just 3% which will increase the value of courgettes in the United Kingdom by £134,086 (Table 3).

Discussion

The importance of pollinators to courgettes is demonstrated through a significant reduction in fruit size and weight under no-pollination conditions. Consequently, percentage fruit set, the size and weight, but not sugar content, of courgettes were significantly increased with pollination. As all flowers within a field experienced the same environmental conditions, the observed reduction in fruit set (for nonpollinated and open-pollinated flowers) was owing to the absence of pollen. The relatively high fruit set of hand-pollinated flowers (98%) suggests that resources (such as nutrient and water availability) were unlikely to be limiting courgette growth and fruit set, and demonstrates the quality and quantity of courgettes under optimal pollination conditions. Unfortunately, it was impossible to identify any differences in pollinator dependence between courgette varieties, as data from this study are only available for one courgette variety.

Table 2. Results from the GLMMs and LMMs on the effect of distance from the crop edge on field-grown courgette quality and quantity measures (mean ± SE)

Measure	0 m from the crop edge (mean ± SE (*n*))	50 m from the crop edge (mean ± SE (*n*))	Contrast estimate ± SE	Test statistic	*P*-value
Fruit set (%)	92 ± 5.8 ($n = 5$)	97.8 ± 2.2 ($n = 5$)	0–50 m: 0.95 ± 1.64	$Z = 0.576$	0.56
Fruit growth (length in cm after 10 d)	26.3 ± 0.7 ($n = 45$)	24.3 ± 0.9 ($n = 44$)	0–50 m: −2.65 ± 2.39	$T = 1.106$	0.27
Fruit weight (g)	1009.3 ± 53.3 ($n = 45$)	923.1 ± 61.7 ($n = 44$)	0–50 m: −147.51 ± 167.14	$T = 0.883$	0.38
Brix	3.8 ± 0.1 ($n = 45$)	3.9 ± 0.1 ($n = 44$)	0–50 m: −0.12 ± 0.20	$T = 0.615$	0.54

N, the number of fruits analyzed.

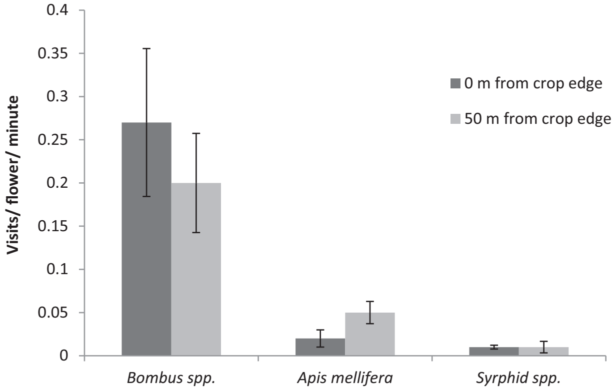

Fig. 2. Flower visitation rate for *Bombus* spp. (*B. terrestris/lucorum*, *B. pascuorum*, and *B. hortorum* combined), *A. mellifera*, and *syrphid* spp. at 0 m and 50 m from the edge of courgette fields in 2016. Mean ± SE ($n = 10$). There was no change in pollinator visitation rate with distance from the edge of the crop (contrast estimate 0.04 ± 0.05 SE, $T = 0.72$, $P = 0.47$).

Nonetheless, it is of industrial and ecological interest that 56% of nonpollinated flowers were still able to reach marketable size and shape without any pollination at all. This is owing to the natural parthenocarpic tendency of courgettes, previously observed in Tosca (Martínez et al. 2013) and other varieties (Robinson and Reiners 1999). However, Martínez et al. (2013) concluded that Tosca was not truly parthenocarpic, as fruits consistently showed a burst in ethylene around 3 d after anthesis, which is thought to cause early fruit abortion in nonpollinated flowers. This may explain the slower growth rate around 3 d postanthesis (Fig. 1) and reduced fruit set in nonpollinated flowers (Table 1). The effect of parthenocarpy appeared to have no effect of sugar content in courgettes, unlike observations in melon (Hayata et al. 2000, Shin et al. 2007).

The level of open pollination at the study sites was very high, evidenced by no statistical difference in yield (length grown, circumference, and weight) of open- and hand-pollinated crops, and an average pollination deficit of just 3%. Similarly, distance from the edge of the crop had no effect on yield (length grown, weight, and °Brix) of open-pollinated courgettes, likely related to no difference in bee visitation at 0 m and 50 m from the crop edge (Fig. 2). This may be because 50 m from the crop edge is not far enough from natural or seminatural habitat (such as hedgerows) to detect differences in pollinators. This is to be expected given that even "door-step foragers" such as *Bombus muscorum* (L.), *Bombus pascuorum* (Scopoli), and *Bombus lapidarius* (L.) are known to forage at distances greater than this (Walther-Hellwig and Frankl 2000, Darvill et al. 2004, Knight et al. 2005). Distance from the edge of the crop is unlikely to be a problem for the majority of cucurbit fields in Cornwall, where the average distance to the center of a field is around 100 m (average field size of 5.2 ± 1.3 ha (S.E.)), but could be more likely for cucurbit fields in Cambridgeshire where the average distance to the center of a crop is around 200 m (average field size of 16.5 ± 3.1 ha). Likewise, spatial and temporal variation in the landscape surrounding each field may influence the level of open pollination. For example, other studies have demonstrated that sites situated nearer to natural and seminatural habitat are more likely to have a greater species richness of pollinators and higher pollination rate (Kremen et al. 2004, Morandin and Winston 2006, Garibaldi et al. 2011). Studies have also shown that larger fields (particularly towards the centre) are more likely to have lower species richness and reduced pollination rate (Artz et al. 2011, Garibaldi et al. 2016).

High levels of open pollination observed in this study are attributed to a high abundance, but not diversity, of pollinators, as *B. terrestris/B. lucorum*, *Bombus hortorum* (L.), *B. pascuorum*, and *A. mellifera* were the only bee species recorded (Fig. 2). This highlights that only a few abundant species, rather than high species richness (contrary to a previous study on pumpkins (Hoehn et al. 2008) and watermelons (Kremen et al. 2002)), can deliver pollination services to a whole crop (Kleijn et al. 2015, Winfree et al. 2015). However, any loss of these functionally important species could greatly reduce pollination services (Larsen et al. 2005). Fortunately, these species are generally widespread, resilient to agricultural expansion, and can be encouraged through simple conservation measures (Kleijn et al. 2015). Observations of pollinator visitation and yield in this study also show that the pollination requirements of courgette can be fulfilled without squash and gourd bees (belonging to the genera *Peponapis* and *Xenoglossa*) which have previously been regarded as the most important pollinators of *Cucurbita* crops in North America (Hurd et al. 1974).

Because courgette yield is dependent on pollination ($D = 0.41$), the total EV of insect pollination to courgettes is estimated to be worth ~£3,398/ha and is consequently a significant proportion of the total EV of courgettes (Table 3). Owing to high levels of open pollination observed in Cornwall, pollination deficit was estimated to be just 3%. Nevertheless, if pollination was maximized, the EV of courgettes would increase by ~£166/ha. This is similar to the apple variety 'Cox' which has an estimated pollination deficit of £146/ha in the United Kingdom (Garratt et al. 2014). Interestingly, this was partly owing to no significant difference between the yield of open-pollinated and pollinator-excluded flowers, which demonstrate the ability of the Cox variety to set fruit in the absence of pollinators. However, the same study showed that the 'Gala' variety had a much higher pollination deficit of £6,459/ha, owing to an increased dependency of this variety on pollination and higher yield from hand-pollinated flowers. This demonstrates how important it is to include different pollinator dependency ratios based on intervariety differences when performing economic valuations.

Table 3. Calculation of the EV of pollinators to courgette production at a hectare and national scale

	Economic value (£)	
	Per ha	United Kingdom value
Quantity Q (Kg)	19,274	–
Economic value EV (£)	8,288	6,694,632
Total EV of insect pollination $IPEV$ (£)	3,398	2,744,735
Maximum EV of pollination service $MaxEV$ (£)	3,564	2,878,821
Value of pollination deficit $PDef$ (£)	166	134,086

P was 0.43 £/ha (DEFRA 2016). Total area of United Kingdom courgette production is 807.75 ha (Outdoor Cucurbit Growers Group, personal communication 22nd September 2016). D was 0.41 and D_{max} 0.43 calculated from experimental results in Table 1.

The price of courgettes used in this valuation (despite being a seasonal average) is likely to vary in response to the supply and demand of courgettes on the open market (Garratt et al. 2014, Melathopoulos et al. 2015). Consequently, the EV of insect pollination to courgettes presented in this study, tells us our actual and potential dependency on pollinators at this current time, rather than an absolute value. If pollinator populations were to decline in the United Kingdom, the supply of courgettes would decrease, which would increase demand (especially if alternative countries were also unable to meet demands). This would raise the price of courgettes on the open market and increase the total EV of insect pollination.

Potential Management Options

Despite the relatively small pollination deficit in this study, spatial and temporal fluctuations in pollinator populations mean that it may still be beneficial for growers to improve pollination services, even if pollination deficits are owing to natural variation in yield. A relatively quick and simple way of doing this is to use commercial bee species which are known to be effective pollinators of cucurbit crops (Artz and Nault 2011, Petersen et al. 2014).

A longer-term but more sustainable option could be to enhance floral resources, a significant limiting factor in bee populations (Roulston and Goodell 2011). Increased floral resources can attract pollinators to a site and provide resources for both managed and wild bees beyond that of the focal crop (Carvell et al. 2007). Generally, the effectiveness of these measures is moderated more by the surrounding landscape, rather than the size of the area planted (Heard et al. 2007, Batáry et al. 2011), with more simplistic landscapes showing greater yield increases than ones which already have good floral resources. As Cornwall already benefits from biodiverse hedgerows and generally smaller field sizes, availability of floral resources may be strongly influencing the high pollination rates observed in this study and is a clear incentive for growers in this region to maintain and protect these habitats to ensure high and stable pollination services in the future. Growers may also benefit from using crop varieties which have been selectively bred to be fully parthenocarpic (currently not done by commercial growers of courgette), especially in combination with pollinator-supportive practices (Knapp et al. 2016).

In conclusion, although confined to a single geographic region and variety, this study highlights the importance of pollination for improving yields, even when over half of the fruit set can still be achieved via parthenocarpy. Understanding a crop's demand for pollinators can help growers choose what varieties to use. In areas with lower visitation rates, potentially owing to large fields or less natural habitat, growers may wish to increase the supply of pollinators. In doing so, they may increase their agricultural resilience and further their economic advantage.

Realistic estimates of the amount of insect pollination required for optimum fruit set need to account for not only the variability in pollination deficit that might result from variable pollinator densities and environmental conditions, but also the variability in pollinator dependence between varieties of single crop species, for which there is currently little good evidence (Melathopoulos et al. 2015, Knapp et al. 2016, although see Garratt et al. 2014). In the wider context, discussion and strategies for improving horticultural crop production need to incorporate costs and benefits associated with different methods of maximizing pollination, while remembering that factors other than pollination also contribute to fruit set.

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