Accepted refereed manuscript of:

Ellis C, Feltham H, Park K, Hanley N & Goulson D (2017) Seasonal complementary in pollinators of soft-fruit crops, *Basic and Applied Ecology*, 19, pp. 45-55.

DOI: 10.1016/j.baae.2016.11.007

©2016, Elsevier. Licensed under the Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International http://creativecommons.org/licenses/by-nc-nd/4.0/

Seasonal complementary in pollinators of soft-fruit crops.

Ciaran R Ellis[a], Hannah Feltham[a], Kirsty Park[a], Nick Hanley[b], Dave Goulson[c*]

a. **Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, FK9 9LA.**
b. **Department of Geography & Sustainable Development, University of St Andrews, St Andrews, KY16 9AL.**
c. **School of Life Sciences, University of Sussex, Falmer, Brighton, BN1 9QG**

Running title: Pollinator complementarity and crop yields.

Tables and figures: 7

References: 42

Accepted for publication in *Basic and Applied Ecology* published by Elsevier.

*Corresponding author. Tel.: 01273 678843.

E-mail address: d.goulson@sussex.ac.uk

Abstract

Understanding the relative contributions of wild and managed pollinators, and the functional contributions made by a diverse pollinator community, is essential to the maintenance of yields in the 75% of our crops that benefit from insect pollination. We describe a field study and pollinator exclusion experiments conducted on two soft-fruit crops in a system with both wild and managed pollinators. We test whether fruit quality and quantity is limited by pollination, and whether different pollinating insects respond differently to varying weather conditions. Both strawberries and raspberries produced fewer marketable fruits when insects were excluded, demonstrating dependence on insect pollinators. Raspberries had a short flowering season which coincided with peak abundance of bees, and attracted many bees per flower. In contrast, strawberries had a much longer flowering season and appeared to be much less attractive to pollinators, so that ensuring adequate pollination is likely to be more challenging. The proportion of high-quality strawberries was positively related to pollinator abundance, suggesting that yield was limited by inadequate pollination on some farms. The relative abundance of different pollinator taxa visiting strawberries changed markedly through the season, demonstrating seasonal complementarity. Insect visitors responded differently to changing weather conditions suggesting that diversity can reduce the risk of pollination service shortfalls. For example, flies visited the crop flowers in poor weather and at the end of the flowering season when other pollinators were scarce, and so may provide a unique functional contribution. Understanding how differences between pollinator groups can enhance pollination services to crops strengthens the case for multiple species management. We provide evidence for the link between increased diversity and function in real crop systems, highlighting the risks of replacing all pollinators with managed alternatives.

Keywords: Bumblebee; *Bombus;* pollinator; flies; ecosystem services; farmland biodiversity; pollination ecology

Introduction

Insect-mediated pollination increases yield in around 75% of world food crops, which provide ~35% of our food (Klein *et al.* 2007). The role of wild pollinators in delivering this service is likely to be greater than was previously assumed: a meta-analysis of pollination data from 41 crop systems suggests that honeybees supplement wild pollinator numbers, rather than the other way around (Garibaldi *et al.* 2013) and wild pollinators play a significant role in varied crop systems (e.g. Winfree *et al.* 2008; Breeze *et al.* 2011; Rader *et al.* 2012). Wild species are also important for their contribution to pollinator diversity, which has been shown to positively influence crop yield (Klein, Steffan-Dewenter & Tscharntke 2003). Diversity increases ecosystem service provision when species contribute slightly different functions (Cadotte *et al.* 2011). Particularly, functional diversity is increased when species (or species groups) are complementary in the services they provide. For example, pollinator species may be complementary in the heights at which they forage; honeybees and wild bees are complementary in their use of space on almond trees, so having both groups present increases yield overall (Brittain *et al.* 2013). Likewise seed set in pumpkins grown at different heights was increased when more pollinator groups with different preferred pollinating heights were available (Hoehn *et al.* 2008). For crops with long flowering seasons, one species or group of species may not be active for the entire season, and so complementarity in abundance or activity across time (seasonal complementarity) could be important (Blüthgen & Klein 2011). Species or species groups that overlap in functional contribution may respond slightly differently to changing environmental conditions, thus buffering the overall service over multiple years (Winfree & Kremen 2009; Brittain, Kremen & Klein 2013). Maintaining both complementarity functions and response diversity will ensure that future pollination needs are met under a range of circumstances (Elmqvist *et al.* 2003).

The soft fruit industry in Scotland produces 216,000 tonnes of strawberries (5% of the global total) and 3,000 tonnes of raspberries per year (FAOSTAT). Both crops are highly reliant on insect pollination for marketable fruit. The pollinator requirements of raspberries and strawberries differ:

raspberries are highly attractive to bees and have a short flowering period that coincides with the seasonal peak in bee numbers. Strawberries, on the other hand, have a long flowering season which may require multiple pollinator groups to ensure pollination across the season. This study examines the importance of diversity in soft-fruit pollination by asking the following questions:

1. Are there differences in the response of different pollinator groups to weather and habitat variables which could be important for the continued pollination of these crops?
2. Is there complementarity between different pollinator groups enabling strawberry pollination across the season?
3. Does insect visitation to crop flowers limit the quality and quantity of fruits produced?

Materials and methods

Sites and survey

The main domesticated pollinators on soft-fruit farms are commercially-reared bumblebees. Seven species of wild bumblebees are common in the study area as well as other pollinators including solitary bees, flies and hoverflies (Lye *et al.* 2011). Contact was made with soft-fruit farms in Autumn 2010 and 29 farms were visited in early 2011. Farm managers were asked about commercial pollinator management; how many bumblebee colonies were used and whether, to their knowledge, honeybees were kept within 2 km of the farm. They were also asked about wild pollinator management e.g. whether wild flower strips were grown. Twenty-five farms spread through the regions of Angus, Perthshire and Fife (Fig. 1) were then chosen for inclusion in the field study. Of these nine grew only strawberries, four only raspberries and twelve grew both. Most soft-fruits were grown undercover in polythene tunnels (polytunnels), all of which were open-ended, some were open-sided while others had closed sides. Farmers grew a range of different crop cultivars which could not be standardised.

Pollinator Activity Transects

For each transect (one per farm), a tunnel was picked at random from those with flowering crops and walked at a slow pace, recording all pollinator visits to flowers. Transects on each farm ran for a total of 300m and included between two and four adjacent tunnels. *Bombus* species were classified to species level where possible; workers of domesticated *Bombus terrestris* (L.), wild *B. terrestris* and wild *B. lucorum* (L.) cannot be reliably distinguished by eye. To split the counts of these species into wild and domesticated classifications, we used the average number of *B. terrestris/B. lucorum* observed at farms not using commercial bees divided by the average number of *B. terrestris/B. lucorum* seen at farms using commercial bees to estimate the proportion of *B. terrestris/B. lucorum* observed, that could be attributed to wild sources. These proportions (for each fruit and time period) were then applied to the overall counts on farms using commercial bees, to obtain an estimate of the number of *B. terrestris/B. lucorum* from wild populations versus *B. terrestris* from commercial sources. These calculations assume that the presence of commercial bees does not reduce visitation by wild bees.

Other pollinators were assigned to broad grouping, i.e. bees other than honeybees and bumblebees were all grouped together, as were flies (including hoverflies). Three replicate flowers counts were taken in 1 m^2 areas within each tunnel to estimate floral resources provided by the crop. Cloud cover was estimated as a percentage. Wind speed was estimated on a three point scale (0 = still, 1 = light breeze, 2 = strong breeze), as was rain (0 = no rain, 1 = light rain, 2 = heavy rain). Days with heavy rain were avoided where possible, but if rain began during a visit the transect was completed. Weather stations closest to each farm were used for daily temperature and humidity data. Transects were all walked between 10 am and 5 pm. Farms were visited six times throughout the season, with approximately three weeks between each visit.

Habitat data

Landscape data were obtained from the OS MasterMap Topography Layer (EDINA Digimap Ordinance Survey Service) and ArcGIS 9.2 was used to create circles 1 km around each study site. This corresponds to the approximate foraging range of *B*. *terrestris*, and is probably greater than the foraging range of most other bumblebee species (Knight *et al.* 2005; Osborne *et al.* 2008). The feature classes from the topography layers were reclassified into five categories; (i) urban areas (buildings and structures), (ii) farmland, (iii) water (inland and tidal), (iv) linear man-made structures (roads, tracks and paths); and (v) semi natural habitat (rough grassland, scrub and woodland). The proportions of land cover for each of the five categories within each 1 km buffer were calculated and used in subsequent analysis.

Exclusion experiment

The effect of pollinator visits on fruit quality and weight was evaluated at a subset of the farms (10 raspberry-growing farms and 12 strawberry-growing farms). Pollinators were kept away from flowers using polythene mesh netting (holes 1.35 mm^2, Harrod Horticultural Ltd, Lowestoft, UK). For raspberries, 6 plants were used in each of 3 different polytunnels per farm; on each plant a bunch of approximately 9 unopened flowers were covered with the netting which was secured to the branch with covered wire. The bunches were marked with coloured tape along with a control bunch from the same plant. Strawberry plants were entirely covered with the exclusion mesh which was supported by arches of flexible garden wire. The plants were covered in groups of four (two groups of four were covered in each of two polytunnels). Each group was matched with a group of control plants. Excluded and control fruits were picked when ripe. The picked berries were categorised into class I and class II fruit based on European marketing criteria and weighed (European Commission 2011).

Statistical Analyses

Statistical analyses were conducted using the statistical software R version 2.15.1 using packages lme4 and MASS (R Development Core Team, 2010).

Pollinator activity

Counts of each pollinator group were summed along transects for each time period. With abundance of each pollinator group as the response, GLMM models with Poisson errors were fitted to the data with farm identity as a random factor. Data were overdispersed and so observation-level random effects were included in addition to the farm level random effects (Maindonald & Braun 2010). Potential explanatory variables were split into three sets; observation variables (those variables available for each observation including weather variables, date etc.), management variables and habitat level variables (Table 1). The analysis therefore took a hierarchical approach, with observation level variables and farm level variables (habitat and management variables) (Gelman & Hill 2007). A full observation level model was fitted to each pollinator group on each soft-fruit. This model was reduced by removing non-significant terms ($p>0.10$) and comparing the Akaike Information Criterion (AIC) between models until the model with the lowest AIC was achieved. The management variables and habitat variables were then fitted separately to the most informative observational level model and the two-level models were reduced as before.

Complementarity

Seasonal complementarity can be tested for using a variance ratio test (1) (Schluter 1984; Stevens & Carson 2001; Winfree & Kremen 2009), which is based on the relationship between total variance of M elements and the covariances between them (2). In this case the elements (X) are the abundances of the four pollinator groups through time.

$$C = \frac{Var\left(\sum_i^M [\![Si)]\!]\right.}{\sum_i^M Var(Xi)} \qquad (1)$$

$$Var(T) = \sum_{i}^{M} Var(Xi) + 2 \sum_{i<l}^{M} Cov(Xi, Xl) \quad (2)$$

If the species groups do not tend to covary positively or negatively, the total variance will be equal to the sum of the variance of each element, and hence the test statistic (C) will be close to 1. Test statistics less than 1 imply negative covariance and thus that the pollinator groups have different peaks throughout the season. A test statistic (C) across all the farms was calculated from the raw data. We generated farm level complementarity figures by simulating pollinator abundances by group for six time periods throughout the season. To control for effects of weather we took the average weather variables for each of six time periods and used these to generate 1000 random weather scenarios. These scenarios were used as inputs to the best fitting GLMM model for the abundance of each pollinator group. The complementary figures for each simulated set of pollinator abundances were then calculated. *Sensu* Winfree and Kremen (2009) we then compared the complementarity results for the simulated data using the full model, versus the results from the same models but with the day and day squared terms eliminated (the null model) using Wilcoxon signed rank tests.

Exclusion experiment

Models were fitted to the strawberry and raspberry data sets with fruit quality (with binomial errors) or fruit weight (with Gaussian errors) as response variables and farm identity fitted as a random factor within a generalised linear mixed model (GLMM). For the raspberry data the residual deviance after fitting a GLM was approximately equal to the remaining degrees of freedom; there was little remaining variation to explain through random effects and so a GLMM was not used (Crawley 2002). For all models, treatment (insects excluded vs. not excluded) was included as a factor and the average number of pollinators in the transects walked in the previous 5 weeks included as a covariate, following Lye *et al.* (2011) . To take into account the differences in ability to transfer pollen and the speed at which pollinators work, the abundance counts were multiplied by approximate efficiency factors to provide efficiency-adjusted counts (Isaacs & Kirk 2010); honeybee numbers were reduced by a factor of 0.5 relative to bumblebees (Willmer, Bataw & Hughes 1994) and fly numbers were reduced by a factor of 0.2 to approximately reflect the reduced efficiency of pollination that they provide (Albano *et al.* 2009; Jauker *et al.* 2012)

Impact of complementarity on yield

To assess the importance of different pollinator groups to fruit yield across the season, the GLMM models for wild bumblebees, honeybees and flies were used to simulate pollinator numbers across the season under average conditions. The abundances were summed and adjusted for pollinator efficiency and the total adjusted pollinator numbers at each time point were then used as an input for the fruit quality GLMM. On the basis of discussions with farmers, the threshold for profitability was taken to be an average of 80% first class fruit. Pollinator groups were then deleted one by one from the total set, and fruit quality across the season re-evaluated.

Results

Pollinator Activity Transects

From 15 April to 19 August 2011, we observed 2,478 pollinators visiting strawberries in 129 transects at 21 farms and 4,464 pollinators visiting raspberries in 80 transects at 16 farms. Transects took on average 43 minutes to walk. Pollinators were observed on raspberry transects from mid-May to late July, and on strawberries from mid-April to mid-August. On average four (three to five) repeat raspberry transects were walked on each farm with raspberries, and six (four to six) repeat strawberry transects were walked on each farm with strawberries. Strawberry plants were considerably less attractive to pollinators than raspberry plants, with an average density of 6.4 pollinators per 100 m^2 (mean ± s.d. = 3,556 ± 24 flowers), compared to an average of 18.6 pollinators per 100 m^2 (mean ± s.d. = 1,934 ± 23 flowers) on raspberries. These figures are the equivalent of 0.91 pollinators per 500 flowers for strawberries, and 4.89 per 500 flowers for raspberries. Of 21 farms growing strawberries, 18 (86%) used commercial bumblebees on this fruit. While the majority purchased bumblebees for pollination early in the season (late April to June), 3 out of 18 farms restocked with additional colonies mid-way through the season. In contrast, nine of the 16 farms (56%) growing raspberries used commercial bumblebees on raspberries and these farms only bought bees once at the beginning of the season.

Bombus terrestris/B. lucorum, including commercial bumblebees, provided around half the pollinator visits for both crops averaged across all farms (57% of visits to raspberries and 46% of visits to strawberries, see Table S1 in Supporting Information). We estimated that around 16% of visits to raspberries and 29% of visits to strawberries were by commercial *B. terrestris*, with visits by wild *B. terrestris/lucorum* comprising 41% of visits to raspberries and 18% of visits to strawberries. Honeybees contributed approximately a quarter of visits to both crops (Table S1). Other bumblebee species together comprised 20% of pollinator visits for raspberries and 10% for strawberries; these included *B. lapidarius* (L.), *B. pascuorum* (Scopoli) and *B. pratorum* (L.). *Bombus hortorum* (L.) was seen on raspberries but not strawberries. Hoverflies and other flies made up around 1% of visits to raspberries and 23% of visits to strawberries. Other pollinators were too few to analyse. The pollinator counts were subsequently grouped into wild bumblebees (including our estimate of the number of *B. terrestris/B. lucorum* attributable to wild pollinators), commercial bumblebees (the remainder of *B. terrestris/B. lucorum* visits), honeybees and flies (including hoverflies).

A total of 17 of the 25 farms had wild flower strips on the farm with 11 leaving field margins unmowed to assist pollinators. Neither of these variables predicted the number of wild bumblebees on either raspberries or strawberries (Tables 2 and 3). Farmer management of commercial pollinators did, however, have an effect; estimated bumblebee numbers significantly increased with the number of colonies used on strawberries. Where farmers indicated that there were honeybees within flying distance of the farm, higher numbers of honeybees were seen on both raspberries and strawberries. Honeybees were less likely to be found in polytunnels with closed sides than open sides. Commercial bumblebees, on the other hand, were more abundant in closed sided tunnels, as we might expect.

The factors influencing the abundance of pollinators differed between pollinator groups (Tables 2 and 3). Wild bumblebees, commercial bumblebees and honeybees had similar responses to weather variables, reducing in number with increasing cloud, wind and rain, and increasing with temperature. Flies, on the other hand, seemed to respond in the opposite way, increasing in number with increasing wind, rain and decreasing temperature. Numbers of flies visiting strawberries increased with the proportion of urban area within 1 km of the farm. The probability of presence of honeybees on a farm declined with an increased proportion of natural habitat within 1 km of the farm.

Seasonal complementarity

There were marked differences in the seasonal abundance of the different pollinator groups (Fig. 2, Table S3). As we would expect, commercial bumblebees were estimated to be far more abundant early in the season (April-May), for this coincides with when most commercial nests are deployed. Wild bumblebee numbers and numbers of honeybees peak in mid-season, according with their known biology. Interestingly, numbers of flies were generally low but gradually increased through the year, with a marked spike in numbers at the end of the season (August) when other pollinators were scarce. At the final time point flies comprised 77.4% of all insects visiting strawberries.

The variance of the abundance over time for all species at all farms (*Var* (*T*)) was 45.3 whereas the sum of the individual variances ($\sum Var(Xi)$) was 80.3, giving a variance ratio of 0.56 (see Table S3). A test statistic of below 1 supports the hypothesis that pollinator groups peak at different times across the season. The same conclusion was reached when the simulated values of total pollinator abundance for each farm were analysed: comparing the simulated values with and without individual time components, the simulated values from the full model were 0.77 on average for the closed-sided tunnels (compared to 0.96 for the null model; W= 232183, $p<0.001$) and 0.76 on average for the open sided tunnels (compared to 0.93 for the null model; W = 282753, $p<0.001$). The results were consistent whether the abundance figures were adjusted for efficiency or not (see Table S4).

Exclusion experiment

When pollinators were able to access flowers, a higher proportion of raspberries were first class (Table S2: mean = 91% first class, s.d. = 0.09), than when pollinators were excluded (Table S2: 28% first class, s.d. = 0.09) (Fig. 3A, Z = 10.28, $p < 0.001$). Raspberries were also heavier when pollinators were allowed to forage (Table S2: mean of 3.39g ± 0.68 v 4.70g ± 1.13) (Fig. 3C, t = 2.11, p=0.051). There was no relationship between raspberry quality and the number of pollinators recorded (Fig. 3E (i), Z = -1.21, $p>0.05$).

Excluding pollinators from strawberries caused a decline in fruit quality by approximately 50% (0.4 vs 0.8 fruits reaching 1st class) (Fig. 3B, Z = 10.43, $p < 0.001$). There was no significant difference in the weight of the strawberries grown with or without pollinators (Table S2: mean = 11.2g ± 1.70 v 10.2g ± 1.57) (Fig. 3D, Z = -0.29, $p>0.05$). Total efficiency adjusted pollinator number was a significant predictor of the proportion of first class fruit when pollinators were allowed to forage (Fig. 3F, Z = 2.55, p = 0.011), suggesting that pollination was limiting strawberry yield at some sites.

Impact of complementarity on strawberry yields

In both closed-sided and open-sided tunnels there were insufficient pollinators for a high proportion of first class fruit early in the season, which coincides with commercial bumblebee use (Fig. 4). The proportion of first class fruit in the mid-season is predicted to be low in closed sided tunnels if wild bumblebees are not present as honeybees (the other pollinator group present in abundance in mid-summer) are not abundant in this type of tunnel.

In open-sided tunnels, both honeybees and wild bumblebees pollinate during the middle of the season. Correspondingly the proportion of first class fruit does not drop as severely if wild pollinators are not present.

Flies were predicted to be important for pollination at the end of the season for both tunnel types, and predicted aggregate yield fell on the removal of this pollinator group. In neither tunnel type are pollination visits sufficient for 80% pollination across the whole season, but with all pollinator groups present this target was more likely to be hit. Simulations were not run for raspberries as the quality and weight of raspberries was consistently high at all farms sampled, suggesting that pollination services are not limiting raspberry production.

Discussion

The pollination of strawberries throughout the year is facilitated by seasonal complementarity among both wild and commercial pollinators. Honeybees and wild bumblebees can provide pollination through the peak of the season, June and July, after which flies provide the bulk of insect visits and are likely to be the main pollinators. Seasonal changes in pollinator abundance have been described before (e.g. Pisanty *et al.* 2014), but to our knowledge this is the first evidence for seasonal complementarity impacting positively upon yield. Our data support the suggestion that species diversity can improve ecosystem services by increasing the functional range of the service provided.

Wild bee numbers were sufficient to provide adequate pollination for raspberries. Raspberries are much more attractive to pollinators than strawberries and they have a shorter flowering season, which coincides with the peak of wild bee activity. Despite this, commercially-reared bumblebees were used on half of the sites which grew raspberries. While commercially-reared bumblebees may not be necessary every year, there can be high variation in pollinator services between years; Lye *et al.* (2011) found that raspberry pollination was limited by lack of wild pollinators in an experiment in the same area in 2009. The relative abundance of different species can change dramatically between years as observed on watermelon and oil-seed rape (Kremen, Williams & Thorp 2002). Smoothing out interannual variability in pollination services might be a justification for using domesticated bumblebees for raspberry pollination on the farms studied.

There were differences in the responses of the pollinator groups to weather experienced during the study. Information on response diversity could be critical to managing pollination services over time; if a species of pollinator were to decline in abundance or reduce activity due to poor weather conditions, pollination may fall below the threshold required for a profitable harvest. In our system, this is particularly important for strawberries; even during May and June, the threshold for a profitable strawberry harvest was only just met by wild pollinators on the average farm. If different pollinator groups respond differently to weather conditions, the risk of pollination falling too low could be reduced by ensuring the presence of a diversity of species (Elmqvist *et al.* 2003). However, the bees in our study responded in the same way to weather variables; both bumblebee and honeybee activity was reduced with higher wind, rain and cloud cover. Conversely, flies seemed to respond in the opposite way to both *Bombus* and *Apis* bees, and were more likely to be seen on transects in wet weather and higher winds. This may be because flies seek shelter within the tunnels in poor weather, since unlike the social bees they have no nest to retreat to.

Different pollinator groups also responded differently to habitat surrounding the farms. Similar to Steffan-Dewenter and Tscharntke (1999), we found that honeybees were less likely to be observed on a transect with increasing natural habitat in the 1 km surrounding the farm, perhaps because natural habitat provides floral resources that are more attractive to honeybees. No habitat variable tested influenced the numbers of bumblebees in our study. In contrast, fly abundance was positively related to the proportion of urban areas in the surrounding environment. Some fly species are strongly associated with human activity, breeding in organic waste in refuse and compost heaps which may explain this relationship (Goulson *et al.* 2005). Gardens within urban areas may also provide floral resources that support pollinators (Goulson *et al.* 2010), though it was notable that only flies showed a relationship with urban areas in this study.

While farmers could increase the number of commercial pollinators, the wild pollinator management prescriptions (wild flower strips and unmowed field margins) did not increase the visitation rate of any of the pollinator groups. Increasing floral resources has been seen to boost queen numbers in some bumblebees (Lye *et al.* 2009), and is well known to attract large numbers of worker bumblebees (Kells, Holland & Goulson 2001; Carvell *et al.* 2007), but the link to increased pollination of nearby crops is less clear (Klein *et al.* 2012). Feltham *et al.* (2015) found that adjacent wildflower strips boosted visitation of bumblebees to strawberry crops by about 25%, but they did not quantify yield. Many of our farms that had wild flower strips were part of supermarket schemes to boost pollinators, but the area of flowers was generally very small (~0.2 ha) and unlike the situation in Feltham *et al.* (2015) the flower patches were often far away from the crop, with farmers also reporting poor germination of some seed mixes. While such actions, if successful, may contribute to the abundance of pollinators on the farm (Haaland & Bersier 2011), they are unlikely to significantly boost the number of bees on a crop unless they encompass a sizeable area, establish to provide a flower-rich sward, and are near to the crop plant requiring pollination.

Our data suggest that flies may be important pollinators of strawberries in late season since they comprise the large majority of visitors to flowers, although it would be valuable to quantify how effective they are at transferring pollen. Methods to increase fly populations or those of other non-bee pollinators have rarely been studied (although see Hickman & Wratten 1996), though they have been reared for glasshouse pollination (Ssymank et al. 2008). Provision of breeding habitat for flies (which might include dung heaps for many flies or butts of stagnant water for hoverflies such as *Eristalis* sp.) would require little space and minimal maintenance.

Our data suggest that pollination of strawberries is delivered by a suit of wild and managed insects, and that this diversity helps to ensure that there are sufficient insect visitors through the long flowering season and during periods of adverse weather. We argue that more attention should be paid to evaluating the contribution of less-studied pollinators such as flies, which may play a complementary role in ensuring reliable pollination for crops in an uncertain future.

Acknowledgments

The authors wish to thank the farmers and farm workers who allowed access to their land and participated in the survey. We are also grateful to Stuart Bence, Stuart Morrison, Andreia Penado, Emilie Ploquin and Bryony Wallace for their assistance in the field. This work was supported in part by BBSRC grant BB/J014753/1.

References

Albano, S., Salvado, E., Borges, P.A.V. & Mexia, A. (2009) Floral visitors, their frequency, activity rate and index of visitation rate in the strawberry fields of Ribatejo, Portugal: Selection of potential pollinators. part 1. *Advances in Horticultural Science,* **23**, 238-245.

Blüthgen, N. & Klein, A. (2011) Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic and Applied Ecology,* **12**, 282-291.

Breeze, T.D., Bailey, A.P., Balcombe, K.G. & Potts, S.G. (2011) Pollination services in the UK: How important are honeybees? *Agriculture Ecosystems & Environment,* **142**, 137-143.

Brittain, C., Kremen, C. & Klein, A. (2013) Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology,* **19**, 540-547.

Brittain, C., Williams, N., Kremen, C. & Klein, A. (2013) Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B-Biological Sciences,* **280**, 20132144.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology,* **48**, 1079-1087.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology,* **44**, 29-40.

Crawley, M.J. (2002) *Statistical Computing: An Introduction to Data Analysis using S-Plus.* Chichester, Wiley.

Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment,* **1**, 488-494.

European Commission. (2011) 543/2011/EU. https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/299247/Strawberries.pdf

Feltham, H., Park, K., Minderman, J. & Goulson, D. (2015) Experimental evidence of the benefit of wildflower strips to crop pollination. *Ecology & Evolution* 5: 3523-3530.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhoffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlof, M., Seymour, C.L., Schuepp, C., Szentgyorgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N. & Klein, A.M. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**, 1608-11.

Gelman, A. & Hill, J. (2007) *Data Analysis using Regression and Multilevel/Hierachical Models.* 1st edn. Cambridge, Cambridge University Press.

Goulson, D., Derwent, L.C., Hanley, M.E., Dunn, D.W. & Abolins, S.R. (2005) Predicting calyptrate fly populations from the weather, and probable consequences of climate change. *Journal of Applied Ecology,* **42**, 795-804.

Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L. & Darvill, B. (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology,* **47**, 1207-1215.

Haaland, C. & Bersier, L. (2011) What can sown wildflower strips contribute to butterfly conservation?: An example from a Swiss lowland agricultural landscape. *Journal of Insect Conservation,* **15**, 301-309.

Hickman, J.M. & Wratten, S.D. (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology,* **89**, 832-840.

Hoehn, P., Tscharntke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B-Biological Sciences,* **275**, 2283-2291.

Isaacs, R. & Kirk, A.K. (2010) Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology,* **47**, 841-849.

Jauker, F., Bondarenko, B., Becker, H.C. & Steffan-Dewenter, I. (2012) Pollination efficiency of wild bees and hoverflies provided to oilseed rape. *Agricultural and Forest Entomology,* **14**, 81-87.

Kells, A.R., Holland, J.M. & Goulson, D. (2001) The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation,* **5**, 283-291.

Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B-Biological Sciences,* **270**, 955-961.

Klein, A., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N. & Kremen, C. (2012) Wild pollination services to california almond rely on semi-natural habitat. *Journal of Applied Ecology,* **49**, 723-732.

Klein, A., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences,* **274**, 303-313.

Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, A. & Goulson, D. (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology,* **14**, 1811-1820.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America,* **99**, 16812-16816.

Lye, G.C., Jennings, S.N., Osborne, J.L. & Goulson, D. (2011) Impacts of the use of nonnative commercial bumble bees for pollinator supplementation in raspberry. *Journal of Economic Entomology,* **104**, 107-114.

Lye, G.C., Park, K., Osborne, J., Holland, J. & Goulson, D. (2009) Assessing the value of rural stewardship schemes for providing foraging resources and nesting habitat for bumblebee queens (Hymenoptera: Apidae). *Biological Conservation,* **142**, 2023-2032.

Maindonald, J. & Braun, J. (2010) *Data Analysis and Graphics using R, an Example-Based Approach.* 3rd edn. Cambridge, Cambridge University Press.

Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. & Sanderson, R.A. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology,* **45**, 784-792.

Pisanty, G., Klein, A.M. & Mandelik, Y. (2014) Do wild bees complement honey bee pollination of confection sunflowers in Israel? *Apidologie* **45**, 235-247.

Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A. & Edwards, W. (2012) Spatial and temporal variation in pollinator effectiveness: Do unmanaged insects provide consistent pollination services to mass flowering crops? *Journal of Applied Ecology,* **49**, 126-134.

Schluter, D. (1984) A variance test for detecting species associations, with some example applications. *Ecology,* **65**, 998-1005.

Ssymank, A., Kearns, C.A., Pape, T. & Thompson, F.C. (2008) Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. *Biodiversity*, **9**, 86–89

Steffan-Dewenter, I. & Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia,* **121**, 432-440.

Stevens, M.H.H. & Carson, W.P. (2001) Phenological complementarity, species diversity, and ecosystem function. *Oikos,* **92**, 291-296.

Willmer, P.G., Bataw, A.A.M. & Hughes, J.P. (1994) The superiority of bumblebee to honeybees as pollinators - insect visits to raspberry flowers. *Ecological Entomology,* **19**, 1365-2311.

Winfree, R. & Kremen, C. (2009) Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B-Biological Sciences,* **276**, 229-237.

Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology,* **45**, 793-802.

Table 1. List of variables used in GLMMs to explain pollinator visitation to strawberries and raspberries

Observation level	***Farm Level***	***Farm Level***
	Management variables	Habitat variables
Day (from 15 April = 1)	Honeybees within 1 km of farm (Yes or No)	% Woodland and scrub within 1 km
Day squared	Number of bumblebee colonies used on crop per year	% Urban area within 1 km
Time of day	Wild flower strips planted (Yes or No)	% Roads within 1 km
Polytunnel type	Field margins left unmowed (Yes or No)	
Wind speed (0, 1, 2)		
Cloud cover (%)		
Humidity (%)		
Temperature (^oC)		

Table 2. Coefficients and standard errors for variables in the most informative observational model (lowest AIC) explaining number of visits by pollinator groups to strawberry flowers

Strawberries	***Observation level variables in best fit model***								
Pollinator group	Day	Day squared	Polytunnel	Flowers	Cloud cover (%)	Wind (0,1,2)	Rain (0,1,2)	Temp (^{o}C)	Humidity (%)
Wild bumblebees	0.42±0.17*	-1.31 ± 0.15***	-0.20 ± 0.21	0.27 ± 0.11**	-0.22 ± 0.10*	-0.42 ± 0.13**	-0.84 ± 0.35*	0.20 ± 0.12	ns
Commercial bumblebees	-0.98±0.15***	ns	0.11 ± 0.23	ns	ns	-0.28 ± 0.13*	-1.34 ± 0.41**	0.46 ± 0.12***	0.22 ± 0.12
Flies and hoverflies	1.69±0.17***	ns	0.39 ± 0.30	ns	ns	0.61 ± 0.17***	0.41 ± 0.26	-0.34 ± 0.14*	-0.40 ± 0.14**
Honeybees (presence)	ns	-1.34 ± 0.36***	1.28 ± 0.61*	ns	-0.69 ± 0.28*	ns	ns	ns	ns
Honeybees (when present)	0.61±0.18***	ns	1.10 ± 0.47*	ns	-0.41 ± 0.14**	ns	ns	ns	ns

Strawberries	***Farm level variables in best fit model***	
Pollinator group	Management	Habitat
Wild bumblebees	ns	ns
Commercial bumblebees	0.0018 ± 0.000826*†	ns
Flies and hoverflies	ns	0.60 ± 0.21**¶
Honeybees (presence)	ns	-0.16 ± 0.06**§
Honeybees (when present)	1.20 ± 0.56*‡	ns

† Number of colonies bought. ‡ Honeybees known to be deployed nearby (yes or no). ¶ Proportion of urban area within 1 km. § Proportion of natural habitat within 1 km.

Table 3. Coefficients and standard errors for variables in the most informative observational model (lowest AIC) explaining number of visits by pollinator groups to raspberry flowers.

Raspberries	***Observation level variables in best fit model***								
Pollinator group	Day	Day squared	Polytunnel	Flowers	Cloud cover (%)	Wind (0,1,2)	Rain (0,1,2)	Temp (^{o}C)	Humidity (%)
Wild bumblebees	1.48 ± 0.22***	-1.88 ± 0.32***	-0.02 ± 0.20	0.75 ± 0.11***	-0.36 ± 0.11***	ns	ns	ns	ns
Commercial bumblebees	ns	ns	-4.52 ± 1.26***	1.29 ± 0.59*	ns	ns	ns	ns	ns
Honeybees (presence)	ns	ns	1.54 ± 0.71*	0.69 ± 0.44	ns	ns	ns	ns	ns
Honeybees (when present)	1.55 ± 0.54***	ns	0.19 ± 0.42	1.06 ± 0.26***	-0.52 ± 0.26*	1.15 ± 0.30***	ns	0.76 ± 0.26**	ns

Raspberries	***Farm level variables in best fit model***	
Pollinator group	Management	Habitat
Wild bumblebees	ns	ns
Commercial bumblebees	ns	ns
Honeybees (presence)	ns	-0.19 ± 0.08*§
Honeybees (when present)	1.18 ± 0.58*†	ns

.

† Honeybees known to be deployed nearby (yes or no), § Proportion of natural habitat within 1 km.

Fig. 1. Location of study sites within East and South-East Scotland.

Fig. 2. Mean numbers of insects per strawberry transect (numbers stacked to show overall visitation, top line), for simplicity averaged across all farm types. C = Commercial, W = Wild.

Fig. 3. Effect of pollinator exposure and numbers of pollinators (adjusted for efficiency) on fruit quality and weight. Proportion of class I fruit was higher when insects could visit flowers of (A) raspberries and (B) strawberries, weight of fruit was marginally significantly higher when insects could visit (C) raspberries, but insects did not increase weight of (D) strawberries. Fruit quality increased with the number of pollinators adjusted for efficiency in (F) strawberries but not (E) raspberries where no relationship was observed.

Fig. 4. Simulated proportions of class I strawberries across the flowering season with pollinator groups excluded (Exc.). (A) closed-sided tunnels (i) Honeybees kept in the vicinity and (ii) honeybees are not kept within the vicinity. (B) Open-sided tunnels (i) honeybees kept in the vicinity (ii) honeybees not kept in the vicinity. All = all pollinators included.

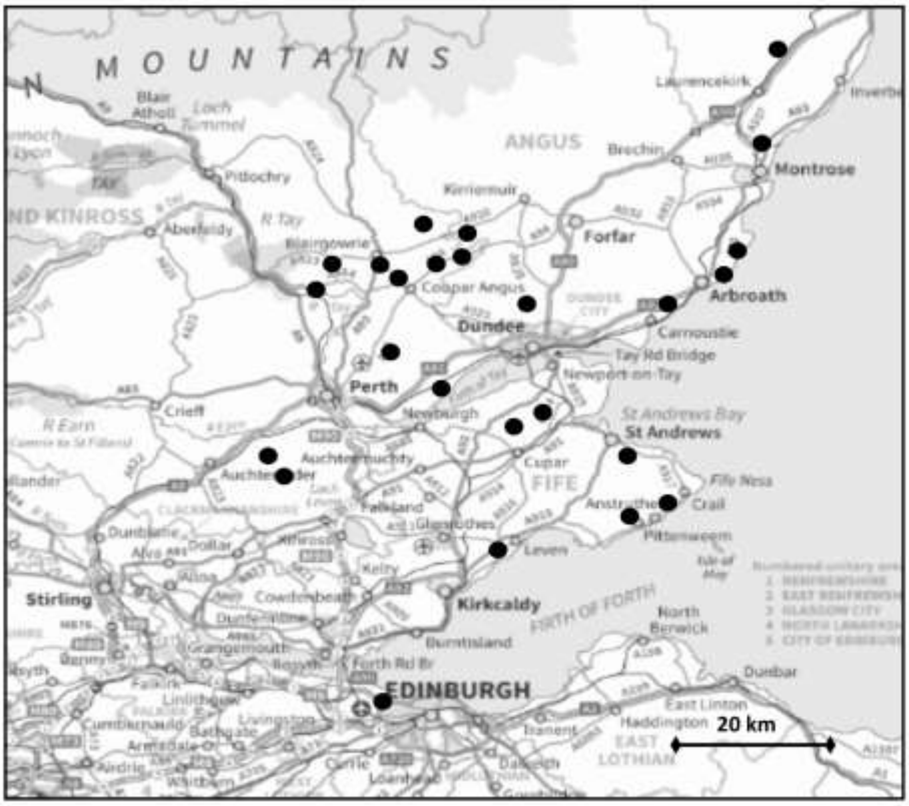
MOUNTAINS
Blair Atholl
Pitlochry
Aberfeldy
ANGUS
Laurencekirk
Montrose
Brechin
Kirriemuir
Forfar
Blairgowrie
Coupar Angus
Arbroath
Dundee
Carnoustie
Tay Rd Bridge
Newport-on-Tay
Perth
Crieff
Newburgh
St Andrews Bay
St Andrews
Auchtermuchty
Cupar
FIFE
Fife Ness
Crail
Pittenweem
Falkland
Glenrothes
Leven
Dunblane
Alva
Dollar
Stirling
Cowdenbeath
Kirkcaldy
FIRTH OF FORTH
North Berwick
Burntisland
Grangemouth
Forth Rd Br
Dunbar
Falkirk
EDINBURGH
Livingston
East Linton
Haddington
20 km
EAST LOTHIAN
Dalkeith
Bathgate
Armadale
Airdrie

Fig. 1.

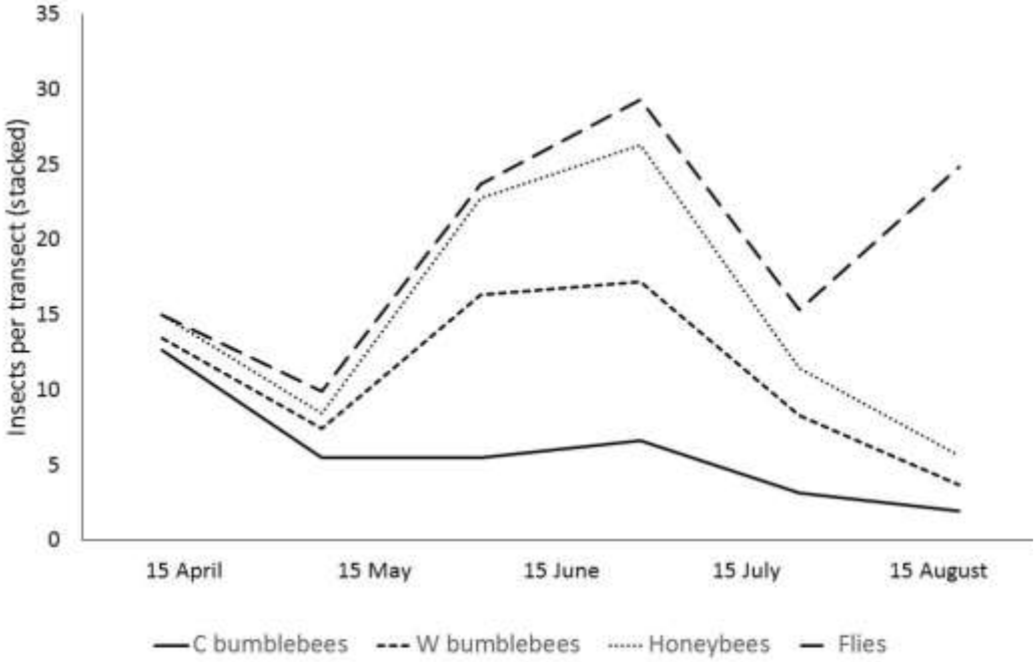
35
30
25
20
15
10
5
0
Insects per transect (stacked)
15 April
15 May
15 June
15 July
15 August
C bumblebees
W bumblebees
Honeybees
Flies

Fig. 2.

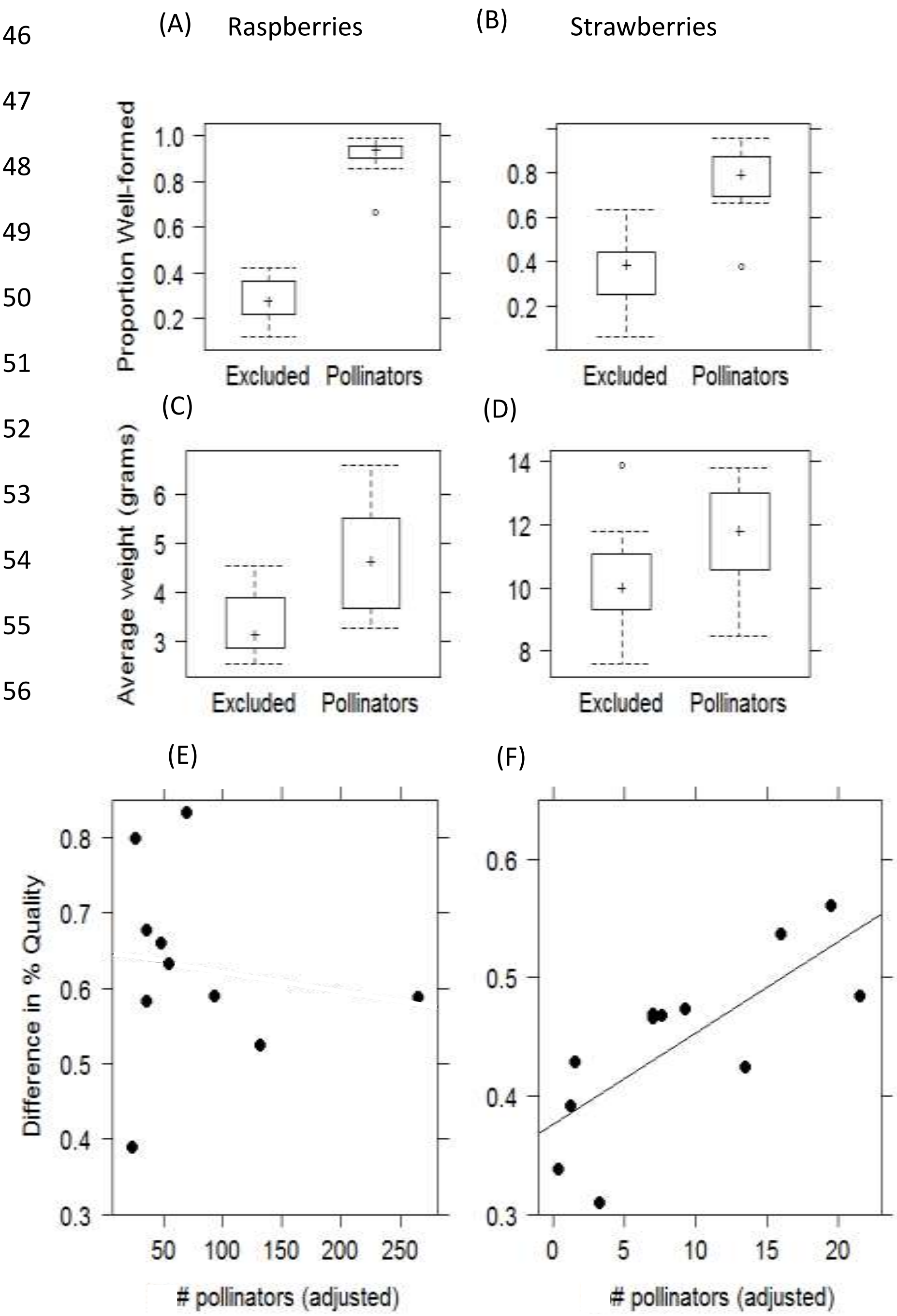
(A) Raspberries
(B) Strawberries
Proportion Well-formed
Excluded
Pollinators
Excluded
Pollinators
(C)
(D)
Average weight (grams)
Excluded
Pollinators
Excluded
Pollinators
(E)
(F)
Difference in % Quality
pollinators (adjusted)
pollinators (adjusted)

Fig. 3.

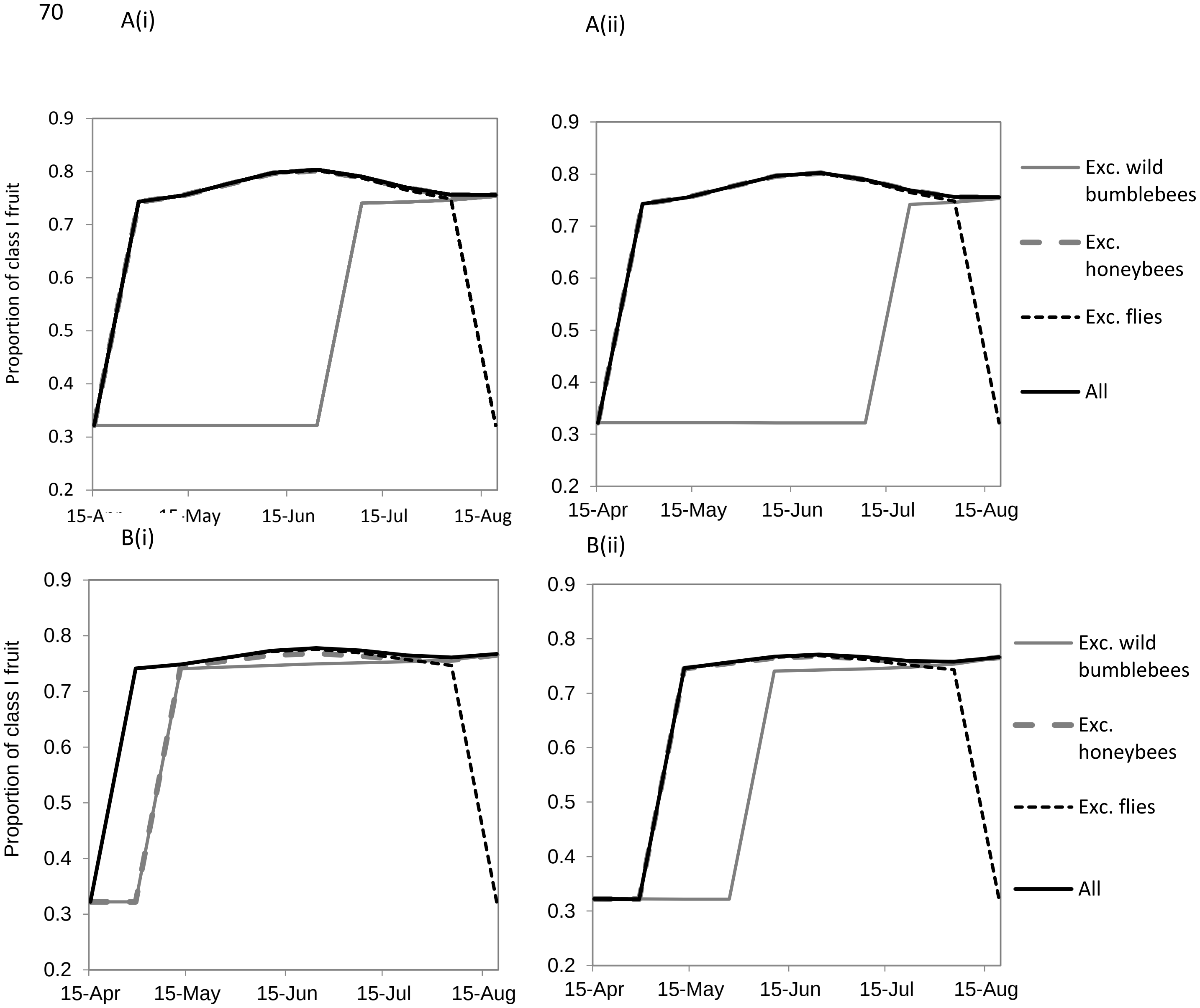
A(i)
A(ii)
B(i)
B(ii)
Proportion of class I fruit
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
15-Apr
15-May
15-Jun
15-Jul
15-Aug
Exc. wild bumblebees
Exc. honeybees
Exc. flies
All

Fig. 4.