Contribution of insect pollinators to crop yield and quality varies with agricultural intensification

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Running title: Pollinator contribution to crop yield

Keywords: agroecosystems, biodiversity, ecosystem services, honeybees, wild bees, pollination.

Data deposition: species richness and abundance of flower visiting insects, and mean crop yield values per site will be deposited in figshare: http://figshare.com/authors/Ignasi%20bartomeus/97352

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.184v1 | CC-BY 3.0 Open Access | received: 31 Dec 2013, published: 31 Dec 2013

Funding: This work was funded by the European Union to the projects "ALARM - Assessing large-scale environmental risks for biodiversity with tested methods" (2003-506675), and "STEP – Status and trends of European pollinators" (244090) in the 6th and 7th Framework Programme, respectively, and by the Swedish research council FORMAS.

Abstract

Background. Up to 75 % of crop species benefit at least to some degree from animal pollination for fruit or seed set and yield. However, basic information on the level of pollinator dependence and pollinator contribution to yield is lacking for many crops. Even less is known about how insect pollination affects crop quality. Given that habitat loss and agricultural intensification are known to decrease pollinator richness and abundance, there is a need to assess the consequences for different components of crop production.

Methods. We used pollination exclusion on flowers or inflorescences on a whole plant basis to assess the contribution of insect pollination to crop yield and quality in four flowering crops (spring oilseed rape, field bean, strawberry, and buckwheat) located in four regions of Europe. For each crop, we recorded abundance and species richness of flower visiting insects in ten fields located along a gradient from simple to heterogeneous landscapes.

Results. Insect pollination enhanced average crop yield between 18 and 71% depending on the crop. Yield quality was also enhanced in most crops. For instance, oilseed rape had higher oil and lower chlorophyll contents when adequately pollinated, the proportion of empty seeds decreased in buckwheat, and strawberries' commercial grade improved; however, we did not find higher nitrogen content in open pollinated field beans. Complex landscapes had a higher overall species richness of wild pollinators across crops, but visitation rates were only higher in complex landscapes for some crops. On the contrary, the overall yield was consistently enhanced by higher visitation rates, but not by higher pollinator richness.

Discussion. For the four crops in this study, there is clear benefit delivered by pollinators on yield quantity and/or quality, but it is not maximized under current agricultural intensification. Honeybees, the most abundant pollinator, might partially compensate the

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loss of wild pollinators in some areas, but our results suggest the need of landscape-scale actions to enhance wild pollinator populations.

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Introduction

There is growing evidence that ecosystem services, such as biological pest control and crop pollination, benefit food production (Bommarco et al. 2013). Indeed, 75% of the crop species used for food depend on insect pollination to some degree (Klein et al. 2007). More than a decade of active pollination research has led to a greatly improved general understanding on animal pollination benefits to crop yields worldwide (e.g., Klein et al. 2007; Garibaldi et al 2011, 2013). However, major knowledge gaps remain.

First, we have surprisingly little information on the actual degree of pollinator dependence for some major crops. While some crops depend entirely on insect pollinator visits to set fruit, many others are only partly dependent on animal pollination and can produce more than 90% of the maximum seed or fruit yield without pollinators (Klein et al. 2007). The role of pollinators for crop production has mainly been examined in observational studies, relying primarily on natural variation in visitation rates among observed sites. Experiments directly manipulating insect flower visitation (e.g., excluded pollinators vs. open access of pollinators) are less common for most crops (but see Klein et al. 2003, Höhn et al. 2008). Assessing pollination dependence with proper controls is needed to correctly estimate the contribution that insect pollinators can provide to crop yields.

Second, most available studies quantify the number of fruits per plant. Fruit number can be a good proxy for yield (Garibaldi et al. 2013), which is the amount of produce harvested per unit area. However, the correlation between the number of fruit produced and yield is likely to be low in some crops. For example, interspecific plant competition can lead to high variability in plant size and thereby fruit production among plants. This is especially critical

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for crops with indeterminate flowering and a high compensation capacity such as soybean (*Glycine max*) and oilseed rape (*Brassica napus*). For these, fruit set measured on a limited number of isolated plants is unlikely to be representative of the real production in a crop stand (Stivers & Swearingin 1980, Angadi et al. 2003). Moreover, plants can allocate resources for producing fruits of variable size based on the number of fruits per plant and the level of pollination received (e.g., Gonzalez et al. 1998 in kiwifruit *Actinidia deliciosa*), such that similar levels of fruit set can differ in total crop yield because of difference in fruit size (Bos et al. 2007). Again, the use of proper control plants from which pollinators are excluded is a way to better estimate the actual contribution of pollinators to yield in such crops.

Quality is also important in crop production, especially from an economic standpoint. Fruit quality can be negatively correlated with quantity when the fruit load on a tree or a vine is too high (e.g., Ferguson & Watkins 1992 in apple *Malus x domestica*), but it is not so otherwise, especially in crops with indeterminate flowering such as oilseed rape (Bommarco et al. 2012). Indeed, adequate pollination often leads to produce with enhanced quality in entomophilous crops such as orchard fruit production (e.g., in apple – Sheffield et al. 2005, Garratt et al. 2014), as well as in field crops (oilseed rape – Bommarco et al. 2012b) and small fruits and vegetables (e.g., strawberry *Fragaria x ananassa* – Andersson et al. 2012, Chagnon et al. 1993, Roselino et al. 2009; tomato *Solanum lycopersicum* – Hogendoorn et al. 2010; bell peppers *Capsicum annuum* – Roldan Serrano and Guerra-Sanz 2006 ; highbush blueberry *Vaccinium corymbosum* – Isaacs and Kirk 2010).

Given the drastic shifts in community composition of insects that visit flowering crops

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(Winfree et al. 2011, Bommarco et al. 2011, Bartomeus et al. 2013a), and declines in pollinator species numbers observed in certain regions (Potts et al. 2010, Carvalheiro et al. 2013), it is increasingly important to gather information on the extent to which different crops depend on insect pollination for yield, and if current pollinator communities fulfill the demand for pollination services such that both crop quality and yields are maximized (Breeze et al. 2011). Relationships between land use intensity, pollinator visitation, and fruit set have been well studied. While pollinator species richness consistently and drastically decays as agricultural landscapes are deprived of natural habitat and are more intensively cultivated (Kennedy et al. 2013), this relationship is much weaker for fruit set (Garibaldi et al. 2011, Chacoff et al. 2008, Ricketts et al. 2008). One explanation for this difference is that the remaining pollinators provide sufficient visitation even in monotonous, intensively cultivated landscapes, especially if the crop has a large degree of autonomous self-pollination. Moreover, intensive landscapes are characterized by harboring just a few generalist pollinator species (Bartomeus & Winfree 2013), but these might be in sufficient numbers to deliver enough crop pollination services. In fact, not all pollinator species respond equally to land use change (Williams et al. 2010, Winfree et al. 2011), and some even increase in abundance with agricultural intensification (Westphal et al 2003, Carré et al. 2009). This diversity of responses can in some cropping systems buffer a loss of pollination function (Cariveau et al. 2013), especially if the pollinators who are the main ecosystem service providers are adapted to the ephemeral and spatially disassociated resource distribution that is typical for agricultural landscapes. Moreover, although wild insects increase fruit set independently of honeybee visits (Garibaldi et al. 2013), honeybees are less dependent on landscape characteristics because they are mainly managed, particularly in North America and Europe, and can be moved around in the landscape.

Hence, honeybees can also help mitigate against wild pollinator loss in more intensively used landscapes where pollination services are degraded. In any case, the composition of the landscape in which the flowering crop field is embedded emerges as an important driver for pollinator community composition, and the landscape context needs to be considered when linking land use to pollination provisioning and benefits in field crops.

Here we used pollinator exclusion on the flowers or inflorescence on a whole plant basis in a set of crops under standard field conditions, to obtain information on pollinator dependency for four economically important annual crops in Europe. We assessed pollinator contribution to both yield quantity and quality. By replicating this experiment along a landscape gradient for each crop, we were able to assess changes in pollinator community composition and visitation rate following landscape level land use change and its consequences for crop pollination services and production.

Material and Methods

Study sites

The fieldwork was conducted in four European countries during May–August 2005 (Table 1). Spring oilseed rape was assessed in the region around the city of Uppsala, Sweden (see Bommarco et al. 2012 for details); field bean (*Vicia faba*) in around Reading, UK, strawberry around Göttingen, Germany; and buckwheat (*Fagopyrum esculentum*) near Krakow, Poland. For each crop, we selected ten fields that were separated by a minimum distance of 3 km, corresponding to the maximum foraging range of most bees (Greenleaf et al. 2007). Within each field, we established a 50 * 25 m study area (5*150 m for buckwheat as the fields were long and narrow) with a homogeneous and continuous crop cover. For fields up to two ha in size, this study site was located in the middle of the field. For larger fields, it was located between the geometric center of the field and one of its margins (Vaissière et al. 2011).

Insect sampling

In each field, we assessed the abundance and species richness of the major groups of flower-visiting insects, including bees (Hymenoptera: Apoidea: Apiformes), hoverflies (Diptera: Syrphidae), and butterflies (Lepidoptera). We used standardized transect walks with an aerial net (Westphal et al. 2008). In each study site, a 150 m transect line was established in the field near the experimental plots. An observer walked this line for 30 min identifying visiting insects at species level and catching unidentified species within a corridor 4 m wide. We performed the transect walks between 0900 and 1700 hours only on days with temperatures at or above 15°C, with no precipitation, dry vegetation, and low windspeed (<40 km.h^{-1}; Westphal et al. 2008). Specimens were pinned, labeled, and subsequently identified to species level. We returned four times to each study site during the main flowering period of each study crop.

Experimental design and yield analysis

In each of the ten fields, we established a block experiment with four blocks. Each block had two treatments with one plot per treatment and five to ten tagged contiguous plants monitored per plot. The first treatment (Open) was open pollinated with all the flowers of each plant accessible to autonomous self-, wind- and insect-pollination. In the second treatment (Net), all flowers were enclosed in nylon tulle bags with 1 * 1 mm openings (Diatex F510; http://www.diatex.fr/-Agriculture-.html) of an appropriate size to cover an

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inflorescence (buckwheat, field bean & oilseed rape), or an individual flower (strawberry). Thus, in the Net-treatment all flowers were exposed to wind- and self-pollination, but not to insect pollination. Because such nets do not hinder the airborne pollen flow (Sacchi and Price 1988, Wragg and Johnson 2011), the difference between these treatments represents the contribution from insect pollination. We put the nets over the flower buds before the onset of flowering. Leaves and plant parts with no flowers were left as much as possible outside the net bag to minimize any effects of the bag on the photosynthesis (Howpage et al. 2001). As soon as flowers had wilted, we removed the nets, and the tagged plants were left to ripen in the field until harvest.

For buckwheat, field bean, and oilseed rape, we cut all experimental plants from each plot and stored them individually in a linen bag just before commercial harvest. For strawberry, we followed the commercial harvest procedure and harvested the ripe strawberries twice a week. In each plot, we recorded the number of fruits per plant (field bean, oilseed rape, and strawberry), and the number and weight of seeds per plant (buckwheat, field bean, and oilseed rape) were measured using a precision scale and a seed counter. For each crop, we also measured the specific attributes of quality that affect its marketing value. For oilseed rape, we analyzed the oil content and chlorophyll contents of the seeds (performed by Svalof Weibull Lab AB, Svalov, Sweden). High chlorophyll contents decrease the durability and alter the color of the extracted oil. For field beans, we measured the nitrogen content of the seed as a proxy of their protein content. The nitrogen content was measured using oxidative combustion in an automated Dumas type combustion analyzer. For strawberry, we classified commercial quality as grade 1 (fully developed fruits of good quality), grade 2 (marketable fruits with some changes in colour and shape) and grade 3 (non-marketable fruits) according to guidelines of the German board of trade. For buckwheat, we measured the proportion of filled seeds since high proportion of empty seeds leads to a penalty in the market price. For buckwheat, six fields where destroyed due to a hailstorm, and hence we do not have yield measures for those.

Landscape context

The ten fields for each crop were located along a gradient of surrounding landscape complexity. The gradient ranged from intensive agricultural landscapes dominated by large arable fields with few boundary features, to complex landscapes with smaller average arable field sizes and more than 40% coverage of semi-natural habitats, such as pastures and forest patches over 0.5, 1, 2, and 3 km radius around each study field. When selecting the field sites, the proportion of arable land in the surrounding landscape was measured around each experimental field and used as a proxy for landscape complexity (Steffan-Dewenter et al. 2002, Fahrig 2013). The proportion of arable land in the landscape surrounding each of the ten experimental fields varied depending on the region, with some regions presenting more intense landscapes (e.g., range of 48 to 97 % of agricultural land for oilseed rape fields at 1000 m radius), and other regions presenting more complex landscapes (range of 4 to 45 % of agricultural land for field bean at 1000 m radius).

For oilseed rape, we used the Swedish digitized land cover terrain map database to characterize the landscape surrounding each field (Lantmateriet 2008). For buckwheat and strawberry, we used CORINE data from 2006 (European Environment Agency: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster-2). For field beans we used the CORINE 2000 Land Cover Map (http://www.ceh.ac.uk/landcovermap2000.html).

Data analysis and statistics

Landscape effects on bee richness and visitation

Because different organisms act in and react to the landscape at different spatial scales, it is necessary to find a suitable scale at which to measure the surrounding landscape (Steffan-Dewenter et al. 2002; Henry et al. 2012). Before exploring any significances, we ran models for each variable with each of the different radii (0.5–3 km) at which the landscapes had been measured. Hence, for each crop we regressed percentage of agricultural area against pollinator richness and abundance at different radii, and identified the radius that explained the highest proportion of variance (highest R^2). For species richness, all crops showed the highest R^2 at a radius of 0.5 km, while abundance was best explained at a 1 km radius with the exception of field bean bee communities, which also responded to a larger scale (1500 m). We performed joint models for all crops at 0.5 and 1 km radius for richness and visitation abundance, respectively. Bee species richness showed a similar relation to landscape complexity for all crops, and this permitted us to include 'crop' as random factor in the model to investigate the general influence of landscape on richness. Visitation abundance, however, followed contrasting trajectories in relation to landscape depending on the crop. We therefore included in the model crop and its interaction with landscape as fixed effects. Pollinator abundances were centered and scaled to a mean of zero and a deviation of one within each crop.

Yield quantity and quality

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We first correlated fruit set with yield (i.e., total fruit or seed weight/plant) for each crop. Block was nested within site and included as random factor in all models. Second, we constructed two mixed effect model with yield as the response variable. In order to analyze all crops in the same model, yield and pollinator visitation abundance were centered and scaled to a mean of zero and a deviation of one within each crop. The first model had pollination treatment, species richness, total visitation abundance, and the interactions of treatment with the other two variables as predictors. The second model had treatment, landscape, and its interaction as predictors. Landscape was investigated at 0.5 and 1 km radius with similar results and so only models at 1 km are shown. Block, nested within site, nested within crop was included as a random factor in all models. In both models, a significant interaction with treatment would indicate that the factor had an effect on yield only in the open treatment. To account for heteroscedasticity, we added a constant variance structure (*varIdent* function in package nlme, R) in which the variance was independently specified for each crop (Cleasby et al. 2011).

We also checked if quality was affected by the pollination treatment. Each crop was analyzed independently due to different measurement units and also because there was no homogeneous response among the crops. Block nested within site was included as a random factor in all models. In this case, we tested only for the effect of the pollination treatment, without including the interactions with species richness, visitation abundance, or landscape context due to sample size limitations. For buckwheat, we used block as a constant variance function to control for the different heteroscedasticity among blocks. The package *nlme* in R was used to fit all models (Pinheiro et al. 2013). Residual plots where used to check for normality and standardized residuals for heteroscedasticity.

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Results

Landscape effects on bee richness and visitation

Pollinator species richness ranged from 2 to 26 species per site (Table 1). The flower visitors of all crops were highly dominated by one or two species of pollinators, in most cases managed honeybees. In field beans, the dominant species were bumblebees; *Bombus terrestris/lucorum* complex, followed by *B. hortorum* and *B. lapidarius* (Fig. 1). Simple landscapes had consistently lower species richness in all crops (GLMM: $F_{1,35} = 5.39$, $P = 0.02$; Fig. 2A). However, the pollinator abundance trend depended on the crop (Table 2; Fig. 2B). Visitation patterns were driven by managed honeybee densities in all crops except for field beans. While in most regions honeybee visits were also higher in complex landscapes (Table 2), in buckwheat there were higher honeybee visits in simple landscapes. For field beans, this positive relationship between number of visits recorded and landscape was even more pronounced at larger scales when we analyze the primary pollinators, the bumblebees, alone ($F_{1,8} = 6.44$, $P = 0.03$ at 1.5 km radius).

Yield quantity and quality

Seed numbers were in all cases positively correlated with yield. However, the correlation was stronger in some crops than others (oilseed rape: $R^2 = 0.95$, $P < 0.0001$; field bean: $R^2 = 0.90$, $P < 0.0001$; strawberry: $R^2 = 0.61$, $P < 0.0001$; buckwheat: $R^2 = 0.67$, $P < 0.0001$).

Open pollination increased fruit set and yield for all crops (Table 3; Fig. 3). We did not detect an interaction between treatment and species richness, which indicates that higher richness does not increase yield in any of the treatments. However, total visitation rate increased yield in both treatments (Fig 4A). Interestingly, landscape complexity (both at 0.5 or at 1 km) also showed a significant interaction with treatment, indicating that simpler landscapes had lower yields only in the open pollinated plants (Table 3; Fig. 4B). However, landscape did not affect the yield of net-bagged plants.

In addition to quantity, the quality of oilseed rape, buckwheat and strawberry increased in the open pollination treatments (oilseed rape: oil content estimate = 1.28 ± 0.31 %, df = 39, t = 4.18 P < 0.001; Chlorophyll content estimate = -4.15 ± 1.76 ppm, df = 39, t = -2.37, P = 0.02; buckwheat: percentage of filled seeds estimate = 0.08 ± 0.01 %, df = 12, t = 6.35, p < 0.001; strawberry: commercial grade estimate = -0.32 ± 0.06, df= 67, t= -5.36, p < 0.001). On the other hand, the nitrogen content of field beans did not increase on open-pollinated plants (estimate = -0.10 ± 0.08 %, df = 37, t = -1.16, p = 0.25; Fig 3).

Discussion

Four economically important entomophilous annual crops in Europe demonstrated highly different degrees of insect pollination dependence. When open pollinated, mean yield increases ranged from 18 to 71% depending on the crop. Three of these crops are listed as having a “modest” positive impact by animal pollination in the comprehensive review by Klein et al. (2007). However, despite being in the same category, oilseed rape and strawberry increased around 20 %, while field bean reached a 40 % increase in yield from insect pollination. The fourth crop, buckwheat is listed as having a large positive impact by animal pollination, in line of our reported 71 % increase. The Klein et al. (2007) review is currently the best available, most up to date source of animal pollination dependence on crops, but our data highlight a disparity of results among crops listed under the same category. Our quantitative data on animal pollination dependence provides a first step to depart from the uncertainty embedded in a categorical approach. For example, animal pollination dependence can change by variety and region. Recent reports show variability in pollinator dependence between 0 to 30% among varieties of oilseed rape (Stanley et al. 2013, Garratt et al. 2013). While we were able to standardize variety for most studied crops, strawberry fields were planted with four different varieties and the presented data should be seen as an average across those varieties (but see Klatt et al. 2013).

As expected, we found that fruit set per plant was positively correlated with yield. However, this correlation was rather weak ($r^2 \sim 0.60$) for both strawberry and buckwheat. This indicates that for these crops, the total fruit weight was quite variable among plants with similar fruit or seed numbers. Indeed, for strawberry, the size of the receptacle is directly related to the number of fertilized achenes while for buckwheat, it is the proportion of filled seeds that can vary considerably and is a major component of yield besides fruit set. While previous research has focused mainly on exploring the effects of pollinators on fruit or seed set (e.g. Garibaldi et al. 2011, 2013), which is a more direct measure of plant reproduction, yield has the potential to better reflect economic value (Bommarco et al. 2012, Klatt et al. 2013), and hence, farmers' interest. For example, while less than 20% in mean yield increase may seem as a modest advantage from the plant perspective, for the farmers it can translate into a substantial difference in revenue.

Similarly, we report that the yield quality component is enhanced to different extents by open pollination in three out of four crops. For buckwheat, strawberry, and oilseed rape, quality is directly linked to the pollinating activity of insects. We find this despite the fact that the measure of quality and underlying mechanisms is specific for each crop, and largely unrelated among crops. Empty seeds in buckwheat accumulate little or no starch (Björkman 1995). The shape of strawberries is also directly related to a complete pollination of all ovules, resulting in a homogeneously pollinated fruit (Zebrowska 1998). For oilseed rape, the plant allocate more oil resources to well pollinated seeds. In contrast, for field beans, the nitrogen content in the seeds was not affected by insect pollination. Other factors such as soil fertility and availability of the appropriate N-fixing bacteria (*Rhizobium* spp.*)* may play a more important role for field beans (Köpke and Nemecek 2010). Is interesting to note that we do not detect any trade-off between yield and nitrogen content of the seeds, as plants with more seeds do not present lower nitrogen content. Hence, the overall protein yield (i.e. nitrogen content at the plant level) was increased with open pollination. On a general note, it is interesting to observe that many different aspects of a plant's investments in its seed or fruit are affected by pollination.

The treatment with netted flowers gives us estimates for the extreme cases where pollinators are completely absent, and we show that the current levels of pollination do not suffice to maximize yield in the open pollinated treatment in all landscapes. As previously reported, we confirm that agricultural intensification has a drastic effect on bee species richness (Rickets et al. 2008, Garibaldi et al. 2011). However, total visitation does not always follow the same pattern as richness. This is the case for buckwheat and field bean, where fields presenting higher total visits were located in simple landscapes. For buckwheat, most of the visits in complex landscapes were due to increased honeybee densities managed for pollination. In field beans we found that bumblebees respond positively to agricultural simplification, noting, however, that even the more simple field beans landscapes contain a fair amount of semi-natural habitats. Overall, we find a general positive relationship between total visitation rates and yield, but not with species richness. If the remaining species that thrive in intensively cultivated agricultural areas, including the managed honeybee, are effective pollinators, yield losses can be partly decoupled from losses of species (Bartomeus and Winfree 2013).

A recent global meta-analysis highlights the role of wild species in crop systems (Garibaldi et al. 2013). The flower visitors of three out of four crops were clearly dominated by honeybees (Fig. 1) and hence, are likely to be key pollinators for those crops. Garibaldi et al. (2013) show that an increase in wild insect visitation enhanced fruit set by twice as much as an equivalent increase in honeybee visitation. While this is generally the case in our target crops (three of which were included as part of Garibaldi's synthesis), the numerical advantage of honeybees in European agricultural landscapes needs to be acknowledged when calculating their total contribution to pollinated plants (e.g., as done in Winfree et al. 2007 and Rader et al. 2009). However, increasing or maintaining high pollinator diversity can enhance yield quantity and stability by improving the pollination efficiency of honeybees (Greenleaf & Kremen 2006) and reduce the risk of pollination failure due to climate change (Rader et al. 2013, Bartomeus et al. 2013b), or environmental disturbances such as extreme weather events (Brittain et al. 2012).

Overall, we also found a weak negative effect of land use intensity on yield (Garibaldi et al. 2011, but see Ricketts et al. 2008), but this was not directly mediated by increased pollinator visitation by itself, because the correlation between pollinator total visits and the proportion of agricultural land in the landscape was weak. The yield of experimental plots with net bagged flowers also increased in sites with more pollinators (Fig 4A). This suggests that other environmental or biotic factors correlated with insect visitation may have been operating simultaneously. The release of airborne pollen by foraging bees could be such a factor (Pierre et al. 2009) (Fig 4B).

In order to make efficient management decisions and increase our power to predict the actual benefit from pollinators in a certain farming situation, we need to estimate the combined contribution of multiple ecosystem services and agricultural inputs (Boreux et al. 2013), as they may be influenced differently by landscape characteristics or have non-additive interactions among them (e.g., Lundin et al. 2013, Martin et al. 2013). Information on the benefit delivered by pollinators to yield quantity and quality in relation to landscape context provides an important baseline for this work.

Acknowledgements

We thank H. Dathe, G. Else, R. Fonfria, S. Iserbyt, M. Kuhlmann, G. Le Goff, D. Michez, H. Mouret, A. Müller, S. Patiny, A. Pauly, P. Rasmont, S. Risch, M. Schwarz, R. Theunert, Waldemar C., and P. Williams for bee identifications to species.

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Table 1. Characteristics of the four study systems.

	Variety	Distance between sites (range in km)	Field sizes (range in ha)	Mean richness of pollinators
Oil seed rape	Stratos	3 - 7	1.0 – 40.4	11.3
Field bean	Clipper	3 - 18	5.0 – 47.0	3.1
Strawberry	Honeoye, Korona, Darselect, Symphonie	3 - 26	0.3 – 1.3	12.9
Buckwheat	Kora	4 - 7	0.3 – 4.0	11.4

Table 2. Effects of land use complexity on total visitation and honeybee visitation (field beans excluded from the honeybee model). Visitation is scaled within each crop. Both models include block nested in site as random factors. Agriculture is the proportion of arable land in the surrounding landscape of each field.

Total visitation	F-value	D.f.	P-value
Crop	3.13	3	**0.04**
Agriculture 1km	0.05	1	0.81
Agriculture*crop	3.08	3	**0.04**
Residuals		32	
Honeybee visitation			
Crop	4.35	2	**0.02**
Agriculture 1km	0.10	1	0.75
Agriculture*crop	3.87	2	**0.03**
Residuals		32	

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Table 3. Effects of open pollination vs pollinator exclusion treatments, visitation and landscape context on yield in four entomophilous crops grown over 10 fields in Europe (buckwheat, field bean, spring oilseed rape and strawberry). Yield and visitation are scaled within each crop. Block, nested in site, nested in crop are included as a random factor. Agriculture is the proportion of arable land in the surrounding landscape of each field.

	F-value	Df	P-value
Pollination treatment	67.05	128	**< 0.001**
Pollinator richness	0.51	28	0.482
Total number of visits	7.25	28	**0.012**
Treatment*Pollinator richness	0.34	128	0.557
Treatment*Total number of visits	0.23	128	0.634
	F-value	Df	P-value
Pollination treatment	10.05	128	**0.001**
Agriculture 1 km radius	0.18	29	0.671
Treatment*Agriculture	9.73	128	**0.002**

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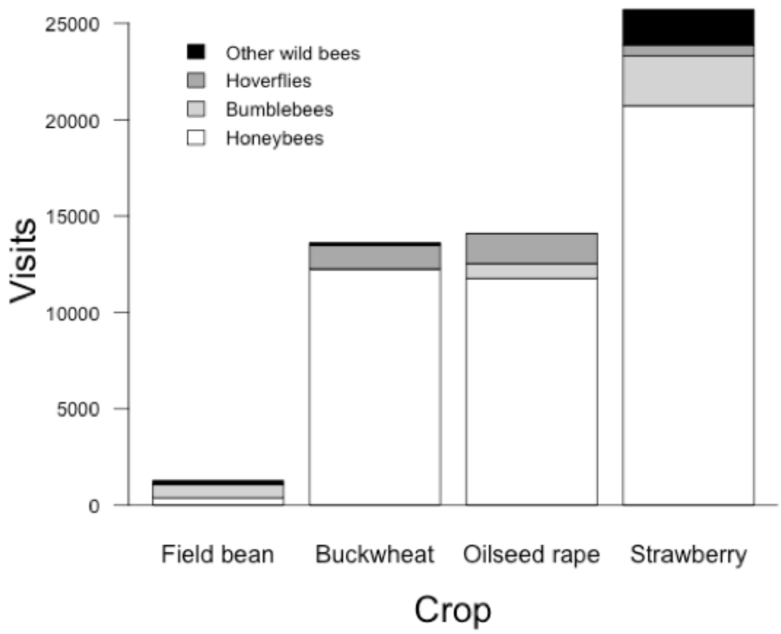
663 **Figures:**

664 Fig 1: Total number of visits recorded per pollinator guild in each crop. All crops received the 665 same sampling effort (i.e., four 30 minutes visits to 150 m transects). Note the strong 666 dominance of honeybees in most crops.



667

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Fig 2: Relationship of A) Pollinator richness per field and B) Total number of visits per field with landscape complexity at the appropriate radii. Each crop individual slope is plotted in a different color and the overall response, when appropriate, in black. Total visits are scaled within each crop.

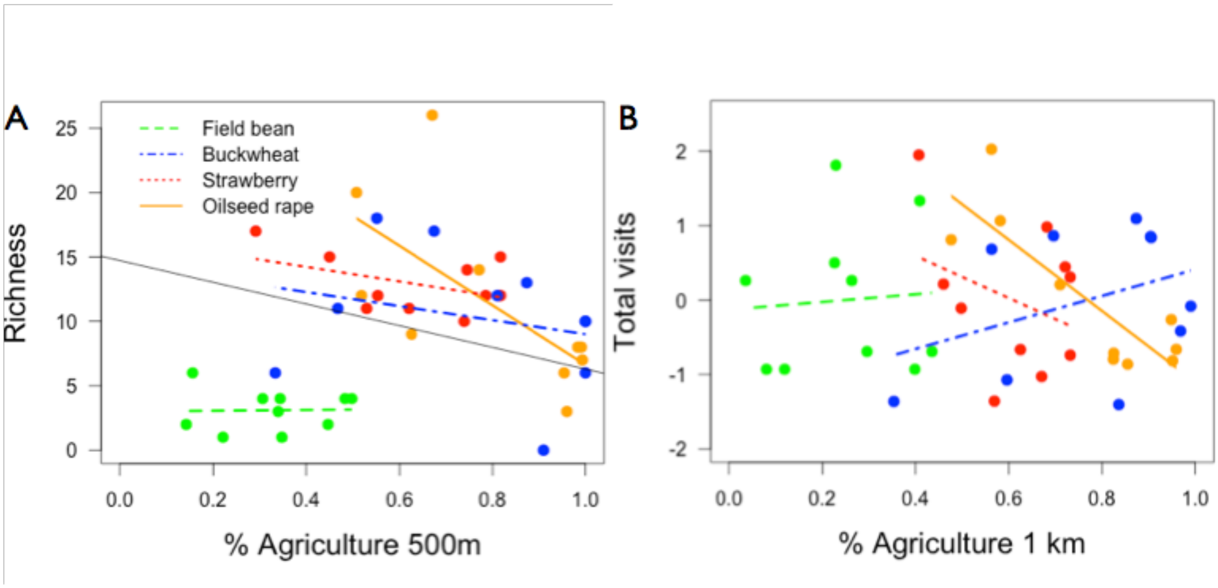

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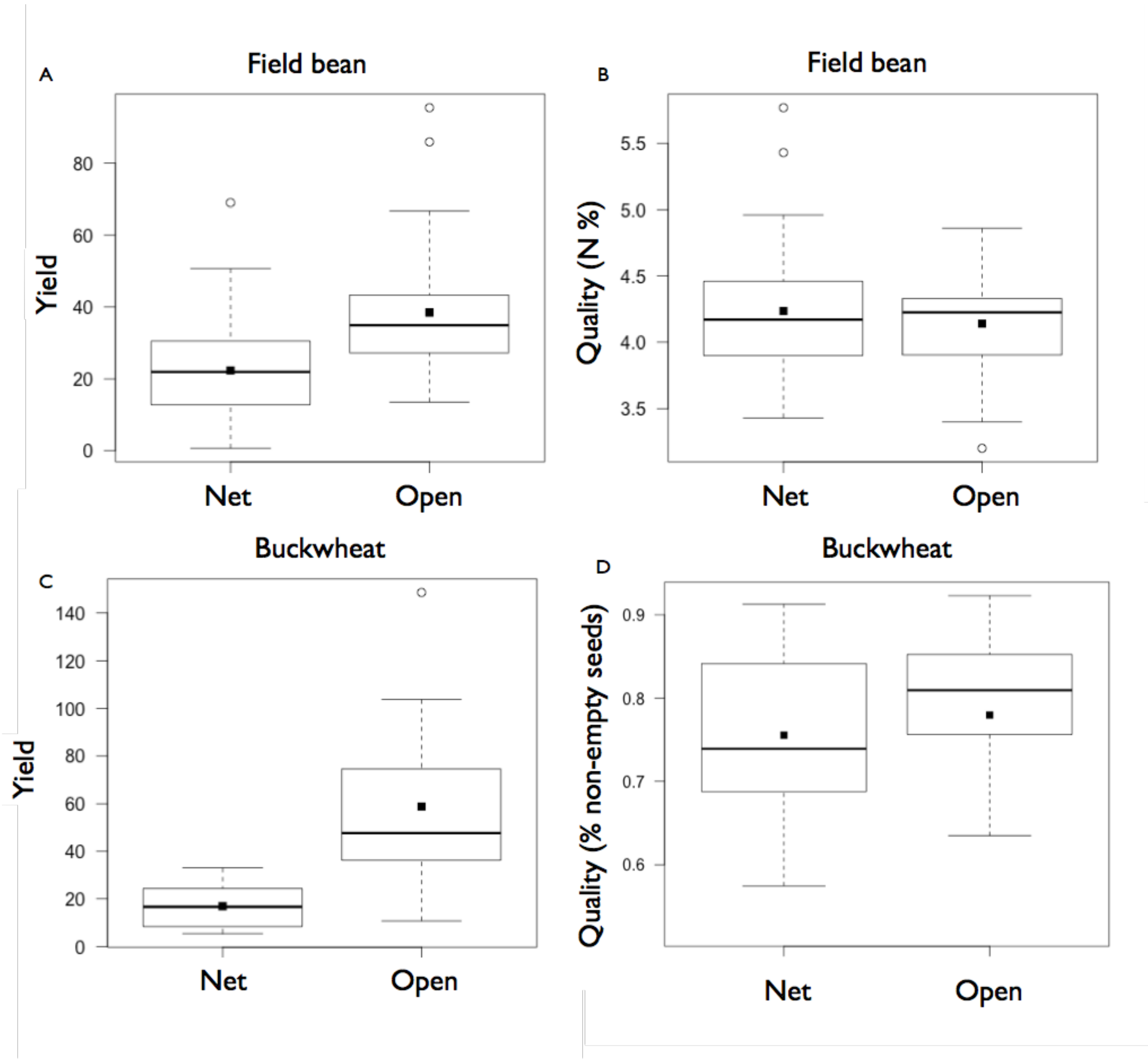
Fig 3: Overall yield per plant (A, C, E, G) and quality (B, D, F, H) with pollinator exclusion (Net) and open pollination (Open) for each crop. Black dots are the mean values reported in the text, and the boxplots reflects the distribution of the data. Yield is measured in seed weight per plant (g) for all crops except strawberry, which was measured as fruit weight per plant (g). Commercial Grades of 1 and 2 are marketable, while grade 3 is considered non marketable.



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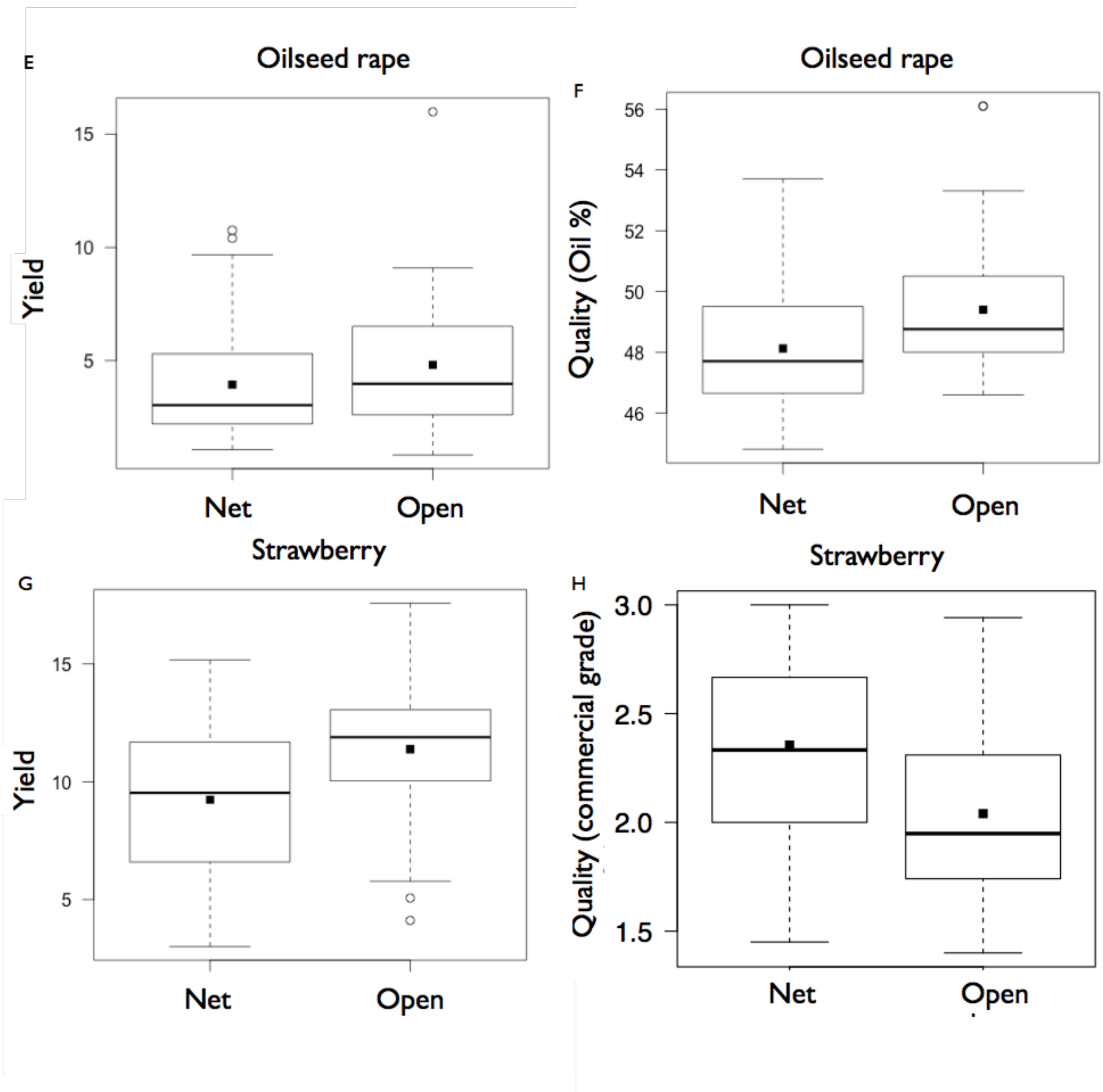
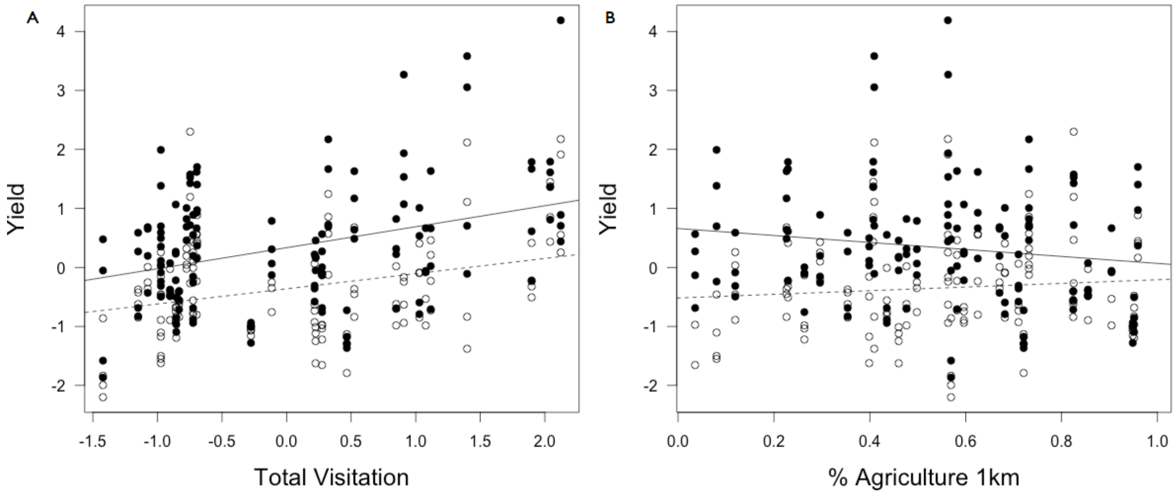


E
Oilseed rape
Yield
15
10
5
Net
Open
F
Oilseed rape
Quality (Oil %)
56
54
52
50
48
46
Net
Open
G
Strawberry
Yield
15
10
5
Net
Open
H
Strawberry
Quality (commercial grade)
3.0
2.5
2.0
1.5
Net
Open

681

Fig 4: Interaction plots showing the relationships of A) Yield per plant and total visitation and B) Yield and landscape complexity for pollinator exclusion (open circles, doted line) and open pollination (black circles, solid line). Total visitation and yield are scaled to a mean of zero within each crop.



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