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## **Predicted thresholds for natural vegetation cover to safeguard pollinator services in agricultural landscapes**

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*Solanum melongena*

## Abstract

The conversion of natural vegetation into cultivated land can cause pollinator declines and thereby degrade pollination services to crops and wildflowers. The effect of landscape composition on pollinator abundance is well established, but its impact on pollination intensity and crop yield is not fully resolved. We therefore studied pollination of two crops in India, brinjal (*Solanum melongena*) and mustard (*Brassica nigra*), along a landscape-scale gradient in habitat transformation from forest-dominated natural vegetation to intensive cultivation. We quantified the pollination requirements (pollen receipt-seed set relationships) of the crops and the levels of pollen delivery by their principal pollinators, bees. Combining these with field surveys of pollinator abundance, we modelled the levels of pollination service to fields along the landscape gradient. Projected pollination services declined as the area occupied by natural vegetation decreased. We identified thresholds at which bee pollination no longer supported maximum seed set, which were landscapes with approximately one quarter (27%) of nearby natural vegetation for brinjal fields and one fifth (18%) for mustard. Our findings indicate that preserving or restoring the cover of natural habitats above these minimum thresholds could be a valuable strategy for maintaining pollinator abundance and safeguarding yield in these bee-pollinated crops.

## 1. Introduction

Virtually all ecosystems on Earth have been transformed through human actions (Millennium Ecosystem Assessment, 2005; Dirzo *et al.*, 2014). In terrestrial ecosystems, one of the most important forms of transformation has been the conversion of land from natural vegetation to agriculture (Foley *et al.*, 2005; Krausmann *et al.*, 2013). Nowadays, over one quarter of the terrestrial surface comprises cultivated systems where at least 30% of the land area is under managed production (Cassman and Wood, 2005). The demand for food from the rising global population will continue to drive up agricultural production (Godfray *et al.*, 2010).

Consequently, there is pressure worldwide to further convert natural vegetation to cropland and to increase crop yields by using agrochemical fertilizers and pesticides. However, modifications to landscapes intended to increase food production can degrade ecosystem services to the crops themselves, such as pollination and biological control of pests (Vanbergen and the Insect Pollinators Initiative, 2013; Holland *et al.*, 2016; Senapathi *et al.*, 2017). Insect pollinators are important service providers that support yields in many crops (Kremen *et al.*, 2007). Wild populations of some pollinator species decline as natural vegetation becomes farmland (Potts *et al.*, 2010) and compensating responses by other pollinators may fail to stabilise the overall levels of pollination services (Cariveau *et al.*, 2013). In some cases (e.g. production of almonds in California), insect pollination in farmland can be boosted artificially by introducing managed honey bees (Morse, 1991), but this is laborious and expensive. Consequently, it may be economically beneficial to protect wild pollinators both to support crop production (Morandin and Winston, 2006; Garibaldi *et al.*, 2013) and also to provide biological insurance against a future loss of honey bees (Winfrey *et al.*, 2007).

Tillage, harvesting and pesticide treatments can reduce the ability of crop fields to sustain wild pollinator populations (Tscharrntke *et al.*, 2005). In farmland, wild pollinators may

persist because of natural habitats or semi-natural habitats (field margins, hedgerows) that occupy interstices between crop fields (Wratten *et al.*, 2012). Interstitial vegetation can provide essential resources to wild pollinators including undisturbed habitat for nesting/hibernation and food (flowers with nectar and pollen) (Holland *et al.*, 2016). Therefore, it would be useful to establish the amount of natural vegetation needed in farmland to ensure that insect pollination does not limit the yields of pollinator-dependent crops. A global synthesis (Kennedy *et al.*, 2013) has linked landscape composition with in-field pollinator abundance, but a similar effort failed to establish its general association with crop yield (Ricketts *et al.*, 2008). If landscape composition affects the level of pollination services, it would be valuable to establish thresholds (i.e. amounts of interstitial natural vegetation) that are required to prevent pollination-limitation of crop yields because this information could be used to guide land management and conservation strategies implemented by farmers and government programs to maintain habitats above the threshold values.

In this study, we investigated variation in pollination service delivery along a landscape-scale gradient in habitat transformation from forest-dominated natural vegetation to intensive cultivation. The levels of pollination service were estimated theoretically from in-field surveys of pollinator abundance using models that we calibrated by experiment (Fig. 1). As a focal system, we studied two bee-attractive crops that are grown by small marginal farms in India: brinjal (eggplant, *Solanum melongena* L.); and yellow sarson mustard (*Brassica rapa* L. cv. 'Yellow Sarson'). Brinjal is the fourth most important vegetable grown in India after potato, onion and tomato and it is an important source of income for marginal farmers (Kumar *et al.*, 2010). Yellow sarson is a self-compatible oilseed that is an energy-rich crop with an important role in human nutrition and animal feed (Mookherjee *et al.*, 2014).

We aimed to quantify site-to-site variation in insect pollination services. Specifically, we estimated levels of pollen delivery by combining observations of flower visitation rates of pollinator taxa with measurements of their per-visit pollen delivery. We then estimated the levels of pollination service to each crop due to pollinator activity by comparing total pollen delivery with the pollination requirements of the two focal crops, which we obtained from experimentally determined pollen receipt-seed set relationships. Finally, we modelled the levels of pollination service in each of a series of fields located along the landscape gradient. When pollen deliveries by insects exactly meet the requirements of seed set so that crop yield is not limited by insect pollination, we can say that the crop receives adequate pollination service. Hence, we tested the hypothesis that levels of pollination service to fields varied with the composition of their surrounding landscape and investigated the minimum thresholds of natural vegetation cover at which crops received adequate pollination services.

## **2. Materials and methods**

### *2.1 Study system*

Our study was carried out in the Balasore district of the Indian state of Odisha, which is in the Lower Gangetic Plain. The climate of Balasore is warm subtropical (typical monthly temperatures range between 21 °C and 31 °C) with seasonal monsoons (annual rainfall c. 1600 mm). Study sites were situated along a gradient of agricultural intensity (Chakrabarti *et al.*, 2015) that stretched approximately west-to-east across a 75 km landscape-scale transect from Nilgiri (21.46°N 86.77°E) to Jaleswar (21°49'N 87°13'E). In general, the study region has a heterogeneous landscape comprising a mosaic of agricultural lands interspersed with natural vegetation, but the relative representation of these elements varied along the landscape transect. At the eastern end of the landscape transect, the landscape is dominated by paddy

fields under high-intensity cultivation regimes (normally three annual harvests) that are supported by the fertile alluvial soil, a network of rivers that supply irrigation and the use of agrochemical fertilizers and pesticides. To the west, the hilly terrain does not provide convenient water for irrigation and the natural vegetation of tropical semi-evergreen forests is punctuated only by small-scale homestead farms under low-intensity cultivation regimes (one annual harvest).

All farms in our study cultivated similar varieties of brinjal and mustard. Across the landscape transect, we studied nine sites with plots of brinjal and fifteen with mustard. Individual sites were separated by at least two kilometres. Collectively, our focal fields varied widely in the representation of nearby natural vegetation (minimum percentage cover = 5%, maximum = 65%), as required. Plot sizes varied between 0.3 ha and 0.5 ha.

Additionally, we established an experimental garden at Panchalingeshwar (21°24' 04.3"N, 86° 44' 27.7" E) that contained varieties of brinjal and mustard typical of the region. We used this garden to quantify certain attributes of the pollination system, such as flower lifetimes and pollinator-specific levels of single-visit pollen deposition (SVD), as described below.

## *2.2 Estimation of pollen delivery to flowers in focal fields*

In order to estimate the overall delivery of pollen to stigmas in a focal field by the local pollinator fauna, we employed a simple model (Primack and Silander, 1975) that quantifies the contribution of each pollinator species by compounding its SVD with its visitation frequency and sums the contributions across the pollinator fauna. Specifically, the amount of pollen delivered by the  $i^{\text{th}}$  pollinator taxon to each flower,  $D_i$ , is given by:

$$G_i = V_i D_i \quad \text{Eq. 1}$$

Here,  $V_i$  denotes the number of times that a receptive flower is visited by individuals of pollinator species  $i$ ,  $D_i$  denotes the expected number of pollen grains that each visit delivers and  $G_i$  denotes the total number of pollen grains a flower receives from the  $i^{\text{th}}$  pollinator taxon. We estimated  $V_i$  by quantifying each of the parameters in the following relationship (Cresswell, 2008):

$$V_i = \frac{B_i}{F} \cdot \frac{L}{H_i} \quad \text{Eq. 2}$$

where  $B_i$  denotes the area density of bees of the  $i^{\text{th}}$  species in the field (bees  $\text{m}^{-2}$ ),  $F$  denotes the area density of the crop's flowers in the field (flowers  $\text{m}^{-2}$ ),  $L$  denotes the receptive lifetime of a flower (hours), and  $H_i$  (hours) denotes the elapsed time between successive flower visits by individuals of the  $i^{\text{th}}$  insect species (i.e. duration of inter-flower travel + duration of handling time per probe). Thus,  $L/H_i$  quantifies the number of visits that a flower could receive if a single bee concentrated on it exclusively and  $B_i/F$  quantifies the number of bees per flower, which is a cardinal indicator of pollinating intensity (Pleasants, 1981). Note that our use of the ratio  $B_i/F$  assumes that bees divide their efforts equally among flowers, which is to assume that foraging is perfectly systematic. The total amount of pollen delivered to flowers in the  $j^{\text{th}}$  focal field by its pollen fauna,  $G_j$ , is given by:

$$G_j = \sum_i D_i V_i \quad \text{Eq. 3}$$

We estimated the number of pollinator visits per flower,  $V$ , by solving Eq 2 for each insect taxon as follows.

To estimate  $B/F$  for each bee species in the crop at each location, we quantified the relative area-densities of bees and flowers in each focal field by establishing two 10 m  $\times$  2 m field-scale transects through the crop. In order to quantify the area density of bees in each field, we walked transects and recorded the number of bees observed per transect. Each walking count yielded a 'snapshot' of the number of bees on the transect, which is not affected by the



specific foraging activity of individuals and does not count individuals twice. At each site, the mean of the counts produced a value for  $B_i$  in units of individuals per  $m^2$ , as required (Eq 2). Observations of visiting pollinators were carried out during peak bloom in nine brinjal fields, which were each surveyed twice in the same year (once in summer, May-June, and again in winter, December-January for two separate plantings) and in 15 mustard fields, which were each surveyed at peak bloom in two successive winters (December-January.) Our insect surveys focused on bees, although some dipteran flies (mainly individuals in Syrphidae and Rhiniidae) were also present (brinjal: 8% of individuals; mustard: 3%). The insect surveys were designed to quantify the average density of bees on flowers across the day and so observations were made repeatedly on the field transects between 7:00 and 13:00 hours in good weather (bright sun, moderate wind). Unidentified insects were collected and preserved in 70% alcohol for subsequent taxonomic identification. In order to quantify the area density of flowers in each field, we counted the number of open flowers in 20 replicate  $1\text{ m} \times 1\text{ m}$  quadrats that were located randomly along each field transect, which yielded a mean value for  $F$  in units of flowers per  $m^2$ , as required, (Eq 2).

In order to determine  $L/H$  (Eq. 2), we made observations in the experimental garden to establish the duration of floral receptivity (hours) and for each bee taxon we observed a number of individuals during a sequence of consecutive visits to the crop's flowers and determined the mean rate of visitation (visits per hour).

To estimate  $G_j$ , the total amount of pollen delivered to flowers by the field's pollinator fauna (Eq 3), we estimated for each bee taxon the mean amount of pollen delivered by a single flower visit (single-visit delivery,  $D_i$ ) by allowing a pollinator to make a single visit to an unpollinated flower (Rader *et al.*, 2013) in the experimental garden. Each experimental flower was obtained by covering a bud with a mesh bag or cage until anthesis and each was presented to a bee before its anthers dehisced to eliminate autogamous pollination. While

standardising the protocol, some bagged stigmas were checked and no pollen was seen on stigmas. To obtain each pollinator visit, we either waited until the focal flower had received an insect visit or, if visits were infrequent, we carried an excised flower to an actively foraging insect as a ‘mobile bouquet’ in a small vase at the end of a cane (Thomson, 1981). After a focal flower had received a single visit, its pistil was carefully removed and placed individually in a sealed vial on damp tissue where it remained for a few hours to enable the compatible pollen to germinate. For each bee species, we counted single-visit pollen depositions (SVDs) to between 10 and 38 flowers (Supplemental Information: Table S1). Subsequently, we made a squash preparation of the stigma (Kearns and Inouye, 1994) and used a microscope and *ImageJ* image-analysis software (Schneider *et al.*, 2012) to count the number of pollen grains attached to the surface of the stigma.

### *2.3 Determination of the pollination requirements of crops*

The pollination requirements of brinjal and mustard were determined by establishing a relationship between the number of pollen grains on a flower’s stigma and the seed set in the resulting fruit using a series of hand-pollinations (Silander and Primack, 1978) in the experimental garden as follows. In each species, we emasculated newly opened flowers by removing their stamens with forceps before pollen release to prevent self-pollination. Contamination by insect pollination was prevented by enclosing each focal flower in an insect-proof cage or mesh bag. For hand-pollination, we collected pollen from at least five different plants and doses from the mixture were dispensed to stigmas from a microscope slide after the number of grains had been counted under a microscope. Specifically, the portion of the slide bearing the defined pollen dose was touched against the stigma to deliver the pollen until transfer was complete, which was checked under a microscope. After the flower had senesced, the mature fruit was harvested and the seeds were counted.

For each plant species, we characterized the pollination-seed set relationship ( $S$  vs.  $G$ , Fig. 2) by using least-squares regression to fit a sigmoidal dose-response relationship of the form:

$$S = \frac{a}{1 + \exp[-b(\text{pollen} - c)]} \quad \text{Eq. 4}$$

We used the best-fit relationships of Eq 4 to estimate the number of pollen grains required for maximum seed set,  $G_{max}$ , for each crop by solving for the number of pollen grains required to produce 99% of the maximum (asymptotic) seed set. We quantify the level of pollination service relative to  $G_{max}$ . When the pollen deliveries by insects equal  $G_{max}$ , we quantify the level of pollination service as 100%. Saturating pollen deliveries above  $G_{max}$  therefore are quantified as greater than 100%.

#### *2.4 Analyzing the relationships between landscape attributes and the intensity of pollination*

To characterize the landscape around each focal field, we examined the land cover in a circular area (two kilometer radius) about its center and estimated the areas covered by natural vegetation based on Landsat TM imagery (30 m resolution) using Arc GIS 10.1 (Environmental Systems Research Institute, Redlands, CA) and Fragstat v.2 software (McGarigal *et al.*, 2012). We quantified the amounts of natural vegetation in each landscape sector by the percentage cover of trees and shrubs, which are likely to be good indicators of the presence of habitat that has not been converted to farmland. The quantification of natural vegetation by its areal cover was designed as a simple proxy measure of the amounts of nesting habitat and floral resources that the habitat provided to bees. The size of the sector was chosen because previous studies indicate that vegetation cover detectably affects the abundance of bees in fields at distances below one kilometre (Taki *et al.*, 2007; Watson *et al.*, 2011) and because the preponderance of bee foraging activity is often within two kilometres of the nest in both honey bees (Schneider, 1989; Visscher and Seeley, 1982) and solitary bees (Gathmann and Tschardt, 2002).

For each crop, we tested the relationship between field-to-field variation in pollination services and the percentage cover of nearby natural vegetation (2 km radius) initially using Spearman's correlation analysis. When a significant trend was revealed, we investigated it by fitting a least-squares regression with a sigmoidal form:

$$\log_{10} \left( \frac{100 \times G}{G_{max}} \right) = k_1 + \left[ \frac{k_2 - k_1}{1 + \exp(-(V - k_3))} \right] \quad \text{Eq. 5}$$

In the regressions, each datum was weighted by the reciprocal of its sampling variance, which we obtained by Monte Carlo resampling (see below). We obtained the threshold level of habitat transformation at which the level of pollination service limited seed set in each crop by solving the best-fit regressions; i.e. we evaluated  $x$  at  $y = 2$ , which is the critical amount of natural vegetation,  $V_{crit}$ , that supports full pollination, i.e. 100% of  $G_{max}$  because  $\log_{10}(100) = 2$ . We note that the three fitted coefficients have biological meaning as follows:  $k_2$ , the proportion of full pollination achieved by a field whose neighbouring habitat is pristine natural vegetation;  $k_1$ , the proportion of full pollination achieved by a field whose neighbouring habitat is denuded of natural vegetation; and  $k_3$ , the proportion of a field's neighbouring habitat that comprises natural vegetation when pollination is half the maximum possible.

To establish confidence intervals on  $V_{crit}$ , we implemented a stochastic Monte Carlo algorithm that recreated our original dataset by sampling from two distributions as follows: (1) we modeled each determination of  $D_i$  as a random sample from a normal distribution with mean and standard deviation set to the taxon-appropriate observed values; and (2) we modeled each field transect survey as a random sample from a Poisson distribution whose parametric mean,  $\lambda$ , was set to the observed value. For each Monte Carlo dataset, the threshold,  $V_{crit}$ , was calculated as for the original observations. The 95% confidence intervals

on  $V_{crit}$  were obtained from sampling distributions each composed of 10000 Monte Carlo values.

All statistical analyses conducted in SPSS (IBM Corp, 2017) except for the Monte Carlo simulations, which were implemented in R (R Core Team, 2013).

### 3. Results

#### 3.1 Pollination requirements of the crops

Seed set increased with the quantity of stigmatic pollen in both brinjal and mustard (Fig. 2).

The total number of grains required for full seed set,  $G_{max}$ , differed substantively between the two species (brinjal:  $G_{max} \approx 94000$  grains per flower, mustard:  $G_{max} \approx 2075$ ).

#### 3.2 Composition and pollinating potential of the bee fauna

Overall, we recorded 10,636 insects visiting flowers on crops in Odisha (brinjal: 1144; mustard: 9492). The pollinator fauna in the focal fields was dominated by two honey bee species (the Asian honey bee, *Apis cerana* Fab. and the giant honey bee, *Apis dorsata* Fab.), which together constituted virtually all flower visitors recorded on both mustard (96%) and brinjal (98%) (Fig. S1). Otherwise, the bee pollinators comprised sweat bees (e.g. the pearly-banded sweat bee, *Nomia* or *Curvinomia*, and *Lasioglossum* sp.), anthophorid bees (e.g. the purple-banded bees), leafcutter bees, and carpenter bees (*Xylocopa* spp.).

On average, bees were three times more frequent on brinjal flowers than in mustard ( $B/F$  ratio: approximately one bee per 330 flowers in brinjal; one bee per 1000 flowers in mustard.)

Our model of flower visitation (Eq 2) predicts that a flower of brinjal received on average approximately 50 visits from bees (SD = 40, n = 9 sites) and a flower of mustard received 25 visits (SD = 20, n = 15) in their receptive periods (brinjal: 21 h; mustard: 18 h).

In both crops, single visit pollen deposition,  $D_i$ , varied approximately fivefold among bee taxa (Table S1). Nevertheless, site-to-site variation in the overall amount of pollen delivered to flowers by insects was principally governed by the expected number of bee visits per flower (regression analysis,  $G_i \sim V_i$ , brinjal:  $r^2 = 99\%$ ; mustard:  $99\%$ ) irrespective of site-to-site variation in the composition of the pollinator fauna.

### 3.3 Landscape composition and levels of insect pollination service

Across the gradient as a whole, mustard received stronger pollination services from bees than brinjal; our model of insect-mediated pollen delivery predicted that receptive flowers of brinjal received on average 70% of the pollen required for full seed set (SD = 59, n = 9 sites) and flowers of mustard received 155% (SD = 117, n = 15).

In both crops, the representation (percentage cover) of nearby natural vegetation was positively associated with the number of bees per flower (Spearman's rank correlation, brinjal:  $\rho = 0.85$ ,  $P < 0.01$ ; mustard:  $0.73$ ,  $P < 0.01$ ; Fig. S2). Similarly, estimated pollen delivery (Eqs 1-3) was positively associated with the representation of nearby natural vegetation (Spearman's rank correlation, brinjal:  $\rho = 0.78$ ,  $P < 0.05$ , Fig. 3; mustard:  $\rho = 0.68$ ,  $P < 0.01$ , Fig. 3)

In brinjal, the pollination-vegetation relationship was well described by a sigmoidal regression (Table S2;  $r^2 = 94\%$ ), which indicated that neighborhoods comprising pristine natural vegetation support pollination services that were one and a half times more than sufficient for maximum seed set in a focal field ( $k_2 = 2.17$ ,  $SE = 0.055$ ,  $10^k = 148\%$ ) and that pollination services in completely deforested neighbourhoods supported about a quarter of maximum seed set ( $k_1 = 1.44$ ,  $SE = 0.066$ ,  $10^k = 28\%$ ). According to the best-fit relationship, the critical threshold of pollination limitation occurred at:  $V_{crit} = 26.5\%$  cover by nearby natural vegetation (Monte Carlo 95% confidence interval: 25.9, 27.1; Fig. 3).

In yellow sarson mustard, the best-fit pollination-vegetation relationship was fairly well described by a sigmoidal regression (Table. S3;  $r^2 = 64\%$ ) which indicated that pristine natural vegetation supported pollination services that were approximately twice that sufficient for maximum seed set in the focal field ( $k_2 = 2.30$ ,  $SE = 0.081$ ,  $10^k = 200\%$ ) and that pollination services in completely deforested neighbourhoods supported about half of maximum seed set ( $k_1 = 1.70$ ,  $SE = 0.110$ ,  $10^k = 50\%$ ). According to the best-fit relationship, the critical threshold of pollination limitation occurred at:  $V_{crit} = 17.5\%$  (Monte Carlo 95% confidence interval: 17.2, 18.1; Fig. 3).

Roughly speaking, our model suggests that adequate pollination services were maintained in landscapes comprising at least one quarter of the natural forest-dominated vegetation nearby to brinjal fields and one fifth nearby to mustard fields.

#### 4. Discussion

We found that farmers in Odisha cannot rely on the local bee fauna to provide adequate pollination services to crops if the natural vegetation cover in nearby landscape falls below 25% for Brinjal and 18% for mustard. Assuming that a ‘space-for-time’ substitution (Pickett, 1989) is appropriate (i.e. our landscape-scale gradient of increasing cultivation represents the potential chronology of an increasingly cultivated site), these thresholds are limits for safeguarding future crop yield against increasing habitat conversion. Robust safeguarding could also involve a variety of additional conservation measures (Garibaldi *et al.*, 2016; Senapathi *et al.*, 2017).

If these thresholds of landscape composition are general, there are consequences for the security of pollination services to crops elsewhere. In Europe, for example, satellite imaging reveals that less than a quarter of agricultural land is occupied by ‘high nature value’ (HNV) farmland in many countries and several others are just above this threshold (Supplemental Information, Fig. S1.) Broadly speaking, HNV farmland is characterized by low intensity farming practices and high biodiversity ecological communities. Reportedly, the share of land area occupied currently by HNV is threatened by changes in agricultural land use (Oppermann and Paracchini, 2012). If the landscape-service relationships that we found in Odisha are taken as a guide, the erosion of HNV in European farmland probably threatens the adequacy of pollination services to crops in many countries. Some important European crops whose yields may be affected detrimentally by pollination limitation caused by the further loss of HNV include those that have either modest pollinator dependence (canola and sunflower) or high dependence (e.g. orchard fruits) (Klein *et al.*, 2007).

We therefore recommend two future steps for safeguarding pollination services to crops in any given country. First, it is necessary to determine thresholds in landscape composition



that safeguard adequate pollination services in the relevant insect-pollinated crops. In particular, it will be valuable to discover whether the proportion of natural habitats necessary to safeguard pollination services is similar to the critical threshold identified in the present study (i.e. about a quarter of the farmland area of pollinator-dependent crops). Second, once thresholds have been identified, it will be possible to identify sub-threshold ‘pollinator deficient’ landscapes and to deploy remedial actions, such as ‘landscape greening’ (Sutter *et al.*, 2018) and enhanced plant diversity (Sutter *et al.*, 2017), in a targeted, economically effective manner.

While our fundamental result is correlative (i.e. the level of pollination services to the crop fields of Odisha declined as the area of nearby tropical forest decreased pollination-natural vegetation relationship), we believe that it is also causal for two reasons. First, the relationship is a general one; pollinator services typically are lower when nearby natural vegetation is sparse (Ricketts *et al.*, 2008; Kennedy *et al.*, 2013; Stavert Jamie *et al.*, 2017). Second, there are plausible underlying mechanisms. One likely cause is that natural vegetation best provides nest sites for wild bee species that pollinate nearby fields (Lonsdorf *et al.*, 2009). For example, the xylocopid bees in our study region nest in rotten wood (Aluri and Rao, 2006), which is probably more prevalent in natural forest than farmland. Also, removal of natural vegetation may harm wild bees by reducing their wildflower forage (Carvell *et al.*, 2017). Moreover, the diminishing representation of natural vegetation is also a proxy for other detrimental factors that are associated with intensive agriculture (Basu *et al.*, 2016). In Odisha, the principal reason for removing natural vegetation is to convert the area to intensively cultivated rice paddies that are protected by agrochemical pesticides. In intensive farmland, the nests of bees often come to contain residues of agrochemicals (Kiljanek *et al.*, 2017) that include harmful insecticides (Goulson *et al.*, 2015). Our observation of fewer bees in more highly cultivated landscapes therefore is not unexpected

given the variety of likely causal drivers (Potts *et al.*, 2010). Additionally, we note that abrupt thresholds in species abundance like those that we observed in bees of Odisha (Fig. S2) occur in other taxa (e.g. woodland birds, see Radford *et al.*, 2005) and are not unexpected across gradients of increasing habitat fragmentation, as for example when a metapopulation experiences the effects of differential habitat connectance (With and Crist, 1995; Keymer *et al.*, 2000).

The pollinator fauna of our focal crops, yellow sarsen mustard and brinjal, was dominated by two species of honey bees, *A. cerana* and *A. dorsata*, which together were over one hundred times more frequent across our study sites than any other pollinator. We found that the species of honey bee in Odisha are similar to European honey bees in serving as effective pollinators of oilseeds and vegetables. For example, the mean single-visit deposits (SVDs) of western honey bees (*A. mellifera*) to flowers in oilseed brassica fields have been recorded in the range of approximately 70-200 pollen grains (Hoyle *et al.*, 2007; Rader *et al.*, 2009; Phillips *et al.*, 2018), which corresponds with our findings (*A. cerana*: c. 130 gains; *A. dorsata*: c. 160). Honey bees typically alight briefly when they visit brassica flowers and larger values of SVDs are evident when honey bees either crawl into tubular flowers, as in pumpkin (*A. mellifera*, SVD  $\approx$  600 grains)(Pfister *et al.*, 2017), or sonicate the flower's anthers, as in brinjal (600-1200 grains, present study).

Together with other similar studies (e.g. Rader *et al.*, 2012; Cariveau *et al.*, 2013), our modelling provides a basis for quantitative approaches to landscape-scale management of pollination services to maintain them at sufficient levels to prevent pollination-limitation of crop yields. Once quantified, the expected amounts of pollen delivered to a stigma by a single bee visit (i.e. SVDs) provide a valuable basis from which to estimate the power of insect pollination services. When combined with observed rates of flower visitation, it is

possible to calculate the overall level of pollen delivery by a pollinator fauna and to investigate the relative importance of its components (Rader *et al.*, 2009; Pfister *et al.*, 2017). Further, estimated pollen delivery can be used to investigate whether insect pollination limits seed set in the focal plant species, which is possible when the relationship is known between stigmatic pollen receipts and a flower's level of seed set. Deposition-seed set relationships have been established in both wild plants (Silander and Primack, 1978) and at least five economically important crops: cranberry (*Vaccinium macrocarpon* Ait.)(Cane and Schiffhauer, 2003), canola (*Brassica napus* L.)(Mesquida and Renard, 1984), Hokkaido pumpkin (*Cucurbita maxima* Duchesne ex Poir cv 'Hokkaido')(Pfister *et al.*, 2017), mustard and brinjal (present study). In some instances, sufficient pollen for complete seed set can be delivered in a single honey bee visit from a bee (cranberry, canola), but other flowers will require either several visits (yellow sarson mustard) or many (pumpkin, brinjal). The likelihood that a flower will be fully fertilised can be derived by estimating the expected number of visits the flower will receive in its receptive lifetime (Cresswell, 2008), which is a function of the relative abundances of bees and flowers ( $B/F$ , Eq. 2) and the lifetime of the flower relative to the rate at which bees can visit flowers ( $L/H$ , Eq. 2). These parameters are relatively easy to estimate and when interrelated by simple mathematical expressions (Eq. 2) it becomes possible to explore the impact of changes in the pollinator fauna either over space (Rader *et al.*, 2012, present study) or over time in hypothetical scenarios, such as bee declines (Pfister *et al.*, 2017). The realized levels of pollinating intensity that can be derived by compounding SVDs with pollinator-specific rates of flower visitation can strengthen the mechanistic basis for understanding plant-pollinator interactions in general (Ballantyne *et al.*, 2015).

Theoretically derived thresholds like those that we have identified will require empirical validation before being used to justify restrictions on land-use intensification. For example, it

is not yet clear that marginally sub-threshold levels of insect pollination in mustard and brinjal would limit seed set because both crops have the capacity for abiotically-facilitated pollination and autonomous selfing (Fig. 1). Specifically, 30% to 60% of brinjal fruit can be set by non-insect modes of pollination (Pal and Singh, 1943). Similarly, most of the agricultural varieties of yellow sarson mustard planted in India are capable of self-fertilization (Hinata and Prakash, 1984) and, like its close relative canola, dense stands in fields are probably pollinated in part by flower-to-flower collisions as the stems sway in the wind (Hoyle *et al.*, 2007). The capacity of some entomophilous (i.e. bee-attractive) crops to pollinate without insects may explain why previous meta-analyses have failed to discover the influence of landscape on yields despite evident effects of landscape composition on pollinator abundance. Therefore, case-by-case testing of putative thresholds in pollinator activity are required by experimental determination of pollinator-limitation of crop yield, which therefore presents an important target for future research.

It is possible that levels of insect pollination in our study system were lower than our estimates because our modelling assumed that flower visitors foraged perfectly systematically (Eq. 2), so that visits are distributed evenly among flowers. If bees instead visit flowers at random according to a Poisson distribution, a flower has a 95% chance of being visited only provided that the expected number of flower visits is approximately three; i.e.  $P(\text{visits} = 0) \geq 0.05$  if  $\text{visits} \sim \text{Poisson}(\lambda \leq 2.996)$ . Hence, if pollinators foraged at random, we have underestimated by threefold the number of visits needed to assure that all flowers are sufficiently pollinated. However, the eusocial bees in Odisha, including the honey bees that dominate the pollinator faunas, are probably adapted to maximize their foraging rate by using various mechanisms to avoid revisiting flowers, such as traplining (Thomson, 1996) and scent-marking flowers (Goulson *et al.*, 1998), which will tend to distribute their visits evenly.

Consequently, we believe that our model will not have greatly underestimated pollen-limitation.

## **5. Conclusions**

In Odisha, the thresholds at which farmers can no longer rely on bees alone to provide crops with a full level of pollination service (i.e. to saturate requirements for seed set) were approximately 25% natural vegetation in brinjal and 17% in mustard. Overall, our study begins to establish a protocol for identifying critical thresholds in landscape composition that, if experimentally validated, could be useful in safeguarding pollinator services to crops.

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## **Declaration of Competing Interest**

None.

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P.B., B.S. and J.C. conceived the study; J.C., A.C, S.C analyzed the data. A.C, S.C., P.B. and J.C. wrote the paper. All authors contributed to the design of data collection protocols and A.C, S.C. and P.B. collected the data. All authors contributed to drafts and approved publication.

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## References

- Aluri, J.S.R., Rao, S.P., 2006. Nesting habits, floral resources and foraging ecology of large carpenter bees (*Xylocopa latipes* and *Xylocopa pubescens*) in India. *Curr. Sci.* 90, 1210-1217.
- Ballantyne, G., Baldock, K.C.R., Willmer, P.G., 2015. Constructing more informative plant-pollinator networks: visitation and pollen deposition networks in a heathland plant community. *P. Roy. Soc. B* 282, 20151130.
- Basu, P., Parui, A.K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S., Smith, B., 2016. Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. *Ecol. Evol.* 6, 6983-6992.
- Cane, J.H., Schiffhauer, D., 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). *Amer. J. Bot.* 90, 1425-1432.
- Cariveau, D.P., Williams, N.M., Benjamin, F.E., Winfree, R., 2013. Response diversity to land use occurs but does not consistently stabilise ecosystem services provided by native pollinators. *Ecol. Lett.* 16, 903-911.
- Carvell, C., Bourke, A.F., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Sumner, S., Wang, J., Heard, M.S., 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature* 543, 547-549.
- Cassman, K.G., Wood, S., 2005. Cultivated systems. Millennium Ecosystem Assessment. *Ecosystems and human well-being: Current state and trends*. Island Press, Washington, DC.
- Chakrabarti, P., Rana, S., Sarkar, S., Smith, B., Basu, P., 2015. Pesticide-induced oxidative stress in laboratory and field populations of native honey bees along intensive agricultural landscapes in two Eastern Indian states. *Apidologie* 46, 107-129.

- Cresswell, J.E., 2008. Estimating the potential for bee-mediated gene flow in genetically modified crops. In: James, R., Pitts-Singer, T. (Eds.), *Bee Pollination in Agricultural Eco-Systems*. Oxford University Press, Oxford, UK.
- Dirzo, R., Young, H., Galetti, M., Ceballos, G., Isaac, N., Collen, B., , 2014. Defaunation in the Anthropocene. *Science* 345, 401-406.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global Consequences of land use. *Science* 309, 570-574.
- Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipólito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Sáez, A., Åström, J., An, J., Blochtein, B., Buchori, D., García, F.J.C., Oliveira da Silva, F., Devkota, K., Ribeiro, M.d.F., Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Filho, A.J.S.P., Kiill, L.H.P., Kwapong, P., Parra, G.N., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M., Veldtman, R., Viana, B.F., Witter, S., Zhang, H., 2016. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* 351, 388-391.
- 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., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, 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., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tschardtke, 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, 1608-1611.
- Gathmann, A., Tschardtke, T., 2002. Foraging ranges of solitary bees. *J. Anim. Ecol.* 71, 757-764.
- Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: The challenge of feeding 9 billion people. *Science* 327, 812.
- Goulson, D., Hawson, S.A., Stout, J.C., 1998. Foraging bumblebees avoid flowers already visited by conspecifics or other bumblebee species. *Anim. Behav.* 55, 199-206.
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347, 1-16.
- Hinata, K., Prakash, S., 1984. Ethnobotany and evolutionary origin of Indian oleiferous Brassicae. *Indian J. Genet. Pl. Br.* 44, 102–112.
- Holland, J.M., Bianchi, F.J.J.A., Entling, M.H., Moonen, A.-C., Smith, B.M., Jeanneret, P., 2016. Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. *Pest Manag. Sci.* 72, 1638-1651.
- Hoyle, M., Hayter, K.E., Cresswell, J.E., 2007. Effect of pollinator abundance on self-fertilization and gene flow: application to GM canola. *Ecol. Appl.* 17, 2123-2135.
- IBM Corp., 2017. IBM SPSS Statistics for Windows, Version 25.0. . IBM Corp, Armonk, New York.
- Kearns, C.A., Inouye, D.W., 1994. Techniques for pollination biologists. University Press of Colorado.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi,



L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584-599.

Keymer, J.E., Marquet, P.A., Velasco-Hernández, J.X., Levin, S.A., 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.* 156, 478-494.

Kiljanek, T., Niewiadowska, A., Gaweł, M., Semeniuk, S., Borzęcka, M., Posyniak, A., Pohorecka, K., 2017. Multiple pesticide residues in live and poisoned honeybees – Preliminary exposure assessment. *Chemosphere* 175, 36-44.

Klein, A.M., 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. *P. Roy. Soc. Lond. B Bio.* 274, 303-313.

Krausmann, F., Erb, K.-H., Gingrich, S., Haberl, H., Bondeau, A., Gaube, V., Lauk, C., Plutzer, C., Searchinger, T.D., 2013. Global human appropriation of net primary production doubled in the 20th century. *P. Natl. Acad. Sci. USA* 110, 10324-10329.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10, 299-314.

Kumar, S., Prasanna, P., Wankhade, S., 2010. Economic benefits of Bt brinjal - an *ex-ante* assessment. Indian Council of Agricultural Research Policy Brief 34.

- Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., Greenleaf, S., 2009. Modelling pollination services across agricultural landscapes. *Ann. Botany* 103, 1589-1600.
- McGarigal, K., Cushman, S., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst, USA.
- Mesquida, J., Renard, M., 1984. Etude des quantites de pollen deposeses sur les stigmates dans differents conditions de pollinisation: influence sur la production de graines chez le colza d'hiver male-fertile. *P. Vth Int. Symp. Pollination* 19, 351-356.
- Millennium Ecosystem Assessment, 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. Island Press, Washington, DC.
- Mookherjee, S., Malik, G., Bandyopadhyay, S., Mitra, B., 2014. The productivity of *Brassica rapa* var. yellow sarson as influenced by integrated nutrient management practices and seed priming in Eastern Indian sub-Himalayan plains. *SAARC J. Agric.* 12, 106-116.
- Morandin, L.A., Winston, M.L., 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agr. Ecosyst. Environ.* 116, 289-292.
- Morse, R., 1991. Honey bees forever. *Trends Ecol. Evol.* 6, 337-338.
- Oppermann, R., Paracchini, M., 2012. HNV farming - central to European cultural landscapes and biodiversity. In: Oppermann, R., Beaufoy, G., Jones, G. (Eds.), *High nature value farming in Europe*. Verlag Regionalkultur, Ubstadt-Weiher, Germany, pp. 16-22.
- Pal, B.P., Singh, H.B., 1943. Floral characters and fruit formation in the eggplant. *Indian J. Genet. Pl. Br.* 3 45-50.
- Pfister, S.C., Eckerter, P.W., Schirmel, J., Cresswell, J.E., Entling, M.H., 2017. Sensitivity of commercial pumpkin yield to potential decline among different groups of pollinating bees. *Roy. Soc. Open Sci.* 4, 170102.

- Phillips, B.B., Williams, A., Osborne, J.L., Shaw, R.F., 2018. Shared traits make flies and bees effective pollinators of oilseed rape (*Brassica napus* L.). *Basic Appl. Ecol.* 32, 66-76.
- Pickett, S.T.A., 1989. Space-for-Time Substitution as an Alternative to Long-Term Studies. In: Likens, G.E. (Ed.), *Long-Term Studies in Ecology: Approaches and Alternatives*. Springer New York, New York, NY, pp. 110-135.
- Pleasants, J.M., 1981. Bumblebee response to variation in nectar availability. *Ecology* 62, 1648-1661.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345-353.
- Primack, R.B., Silander, J.A., 1975. Measuring the relative importance of different pollinators to plants. *Nature* 255, 143-144.
- R CoreTeam, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., Edwards, W., Westcott, D.A., Cunningham, S.A., Howlett, B.G., 2013. Diurnal effectiveness of pollination by bees and flies in agricultural *Brassica rapa*: Implications for ecosystem resilience. *Basic Appl. Ecol.* 14, 20-27.
- 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? *J. Appl. Ecol.* 49, 126-134.
- Rader, R., Howlett, B.G., Cunningham, S.A., Westcott, D.A., Newstrom-Lloyd, L.E., Walker, M.K., Teulon, D.A.J., Edwards, W., 2009. Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J. Appl. Ecol.* 46, 1080-1087.
- Radford, J., Bennett, A., J. Cheers, G., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds.

- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Potts, S.G., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol Lett* 11, 499-515.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* 9, 671.
- Schneider, S.S. 1989. Spatial foraging patterns of the African honey bee, *Apis mellifera scutellata*. *J. Insect Behav.* 2, 505-521.
- Senapathi, D., Goddard, M.A., Kunin, W.E., Baldock, K.C.R., 2017. Landscape impacts on pollinator communities in temperate systems: evidence and knowledge gaps. *Funct. Ecol.* 31, 26-37.
- Silander, J.A., Primack, R.B., 1978. Pollination intensity and seed set in the evening primrose *Oenothera fruticosa*. *Am. Midl. Nat.* 100, 213-216.
- Stavert J.R., Pattemore D. E., Gaskett A., C., Beggs J., R., Bartomeus, I., 2017. Exotic species enhance response diversity to land-use change but modify functional composition. *P. Roy. Soc. B* 284, 20170788.
- Sutter, L., Albrecht, M., Jeanneret, P., 2018. Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services. *J. Appl. Ecol.* 55, 612-620.
- Sutter, L., Jeanneret, P., Bartual, A.M., Bocci, G., Albrecht, M., MacIvor, S., 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *J. Appl. Ecol.* 54, 1856-1864.
- Taki, H., Kevan, P.G., Ascher, J.S., 2007. Landscape effects of forest loss in a pollination system. *Landsc. Ecol.* 22, 1575-1587.

- Thomson, J.D., 1981. Field measures of constancy in bumble bees. *Am. Midl. Nat.* 105, 377-380.
- Thomson, J.D., 1996. Trapline foraging by bumblebees. 1. Persistence of flightpath geometry. *Behav. Ecol.* 7, 158-164.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8, 857-874.
- Vanbergen, A.J., the Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11, 251-259.
- Visscher, P.K., Seeley, T.D., 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63, 1790-1801.
- Watson, J.C., Wolf, A.T., Ascher, J.S., 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environ. Entomol.* 40, 621-632.
- Winfree, R., Williams, N.M., Dushoff, J., Kremen, C., 2007. Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* 10, 1105-1113.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76, 2446-2459.
- Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E., Desneux, N., 2012. Pollinator habitat enhancement: Benefits to other ecosystem services. *Agr. Ecosyst. Environ.* 159, 112-122.



Fig. 1. Schematic representation of the link between seed set in a bee-attractive crop and the attributes of the landscape that surrounds the field. An individual receptive flower receives  $V_i$  visits from the  $i^{\text{th}}$  pollinator taxon, which depends on the favorability of the particular  $j^{\text{th}}$  landscape, denoted ' $V_i \sim \text{landscape}_j$ '. Each flower visit by pollinator  $i$  deposits  $D_i$  pollen grains on the flower's stigma, so that the collective delivery by the pollinator fauna is  $\sum D_i V_i$ . If the stigma additionally receives  $d$  grains by other means (e.g. wind pollination or autonomous self-pollination), then a total number of pollen grains ( $G_j = d + \sum D_i V_i$ ) will be deposited in landscape  $j$ , and fertilize the flower sufficiently to produce  $S_j$  seeds (this conversion is governed by a dose-response curve, which is displayed here as a relationship between  $x$ -axis: 'grains on stigma' vs.  $y$ -axis: 'seed set'). The relative quality of the  $j^{\text{th}}$  landscape in supporting pollinator-dependent crop yield is determined by the ratio of  $S_j$  to the maximum crop yield,  $S_{\text{max}}$ .

Fig. 2. Relationships between seed set ( $y$ -axis: number of seeds matured per fruit) and the number of pollen grains applied to a flower's stigma in experimental hand-pollinations ( $x$ -axis) in two crop plants, brinjal and mustard. Each symbol indicates the data collected from a single flower. Fitted curves indicate best-fit regressions (least squares) with form: seed set =  $a / (1 + b * \exp(\text{grains} - c))$ ; brinjal:  $a = 1419.9$ ,  $b = 0.00014$ ,  $c = 60212.4$ ,  $r^2 = 0.96$ ; mustard:  $a = 27.6$ ,  $b = 0.00356$ ,  $c = 783.6$ ,  $r^2 = 0.96$ .

Fig. 3. Levels of pollination service to two crops, brinjal (upper panel) and mustard (lower panel), in relation to the proportional cover (%) of natural vegetation surrounding a focal field to a radial diameter of two kilometers ( $x$ -axis). 'Pollination service' ( $y$ -axis) is the ratio (logarithmic scale) of the estimated amount of pollen delivered to the stigma of a single

flower by the crop's pollinator fauna at a single site in relation to the amount of pollen the flower requires for maximum seed set, i.e. the ratio of  $S_j$  to the maximum crop yield,  $S_{max}$  (Fig. 1). The dashed horizontal lines indicate maximum seed set (i.e. 100% pollination service). The intercepts between the best-fit sigmoidal regression (solid black line) and solid vertical lines indicate on the  $x$ -axis a threshold minimum level of natural vegetation that secures an adequate level of pollination service (brinjal, 26.5%; mustard, 17.5%). Error bars indicate 95% confidence intervals.