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Pollination services decline with distance from natural habitat even in biodiversity-rich areas

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Summary

1. There is considerable evidence for the negative impacts of habitat alteration on pollinators in highly disturbed regions of the world. However, it remains unclear whether these findings reflect a global crisis for crop pollination. Understanding the extent to which world agriculture is endangered by pollinator decline is essential if the economic valuation of nature is to be used to promote conservation.
2. We assess the susceptibility to pollinator limitation of one of the most important tropical and subtropical fruit crops, mango *Mangifera indica* L., commonly planted in a region of South Africa located between two large biodiversity-rich protected natural areas. We conducted flower visitor surveys, exclusion experiments and spatial analysis of flower visitation and fruit production patterns.
3. Our results show that both ants and flower visitors were effective pollinators of mango, the latter significantly declining (in abundance and species richness) with distance to natural habitat while ants were not affected. Neither the absence of pesticides nor the supplementation of flower visitors by using managed honeybees served to offset these negative impacts. Food-web data suggest that maintaining diversity of flower resources within farmland can help maintain pollinator communities.
4. Moreover, models based exclusively on pollinator abundance underestimated the negative effect of distance from natural habitat on production (42% less at 500 m from natural habitat). As soil nutrient levels and water content are regularly measured and corrected in all study sites, these results suggest that pollinator diversity may also be important.
5. *Synthesis and applications.* This study provides one of the first examples of marked pollination limitation in farms surrounded by well-protected natural habitat. For mango farming to be sustainable, it is essential to limit contiguous growth of farmland and consider practices that restore the complexity of plant-pollinator networks within farms, for example through the creation and maintenance of pollinator-friendly areas. By highlighting the economic gains of adopting pollinator-friendly practices in agriculture, this work contributes to a growing body of studies that reveal that making farmland more suitable for pollinators benefits both agriculture and nature conservation.

Key-words: agro-ecology, ecosystem services, flower-visitor community, natural habitat conservation, organic farming vs. conventional farming, pollination

Introduction

Habitat alteration is one of the primary causes of pollinator declines, with many examples from highly disturbed areas in the world (e.g. Winfree *et al.* 2009). Such declines have led to concern about the concomitant effects on pollinator-dependent food crop production, which have become increasingly important in human diets (Aizen *et al.* 2008). However, it has been suggested that an agriculture crisis in pollinator-dependent crops is only likely to occur in areas of the world where little natural habitat, and associated insect biodiversity, remains (Ghazoul 2005; Winfree *et al.* 2009).

Although tropical and sub-tropical regions are still relatively rich in natural habitat, economic growth in these regions is driving accelerated replacement of natural areas by

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agricultural landscapes, increasing their susceptibility to pollination problems (e.g. Gemmil-Herren & Ochieng 2008). Farmers worldwide have responded to pollinator limitation by introducing managed flower visitors, such as *Apis mellifera* L. (hereafter referred to as 'honeybees'), within crop fields (Aizen & Harder 2009). Depending on a single pollinator species, however, is inherently risky (Kremer, Williams & Thorp 2002), and for several crops managed species are either unsuitable as pollinators (e.g. Ying *et al.* 2009) or less efficient in the absence of a diverse flower visiting assemblage (e.g. Greenleaf & Kremen 2006). To evaluate the susceptibility of different world regions to crop pollinator limitation, it is crucial to understand how pollinators respond to landscape changes and how these changes affect crop productivity (Kremen *et al.* 2007). This information could also be used to evaluate and improve the global applicability of general scenarios based on spatially explicit models that predict pollination services within agricultural landscapes (Keitt 2009; Lonsdorf *et al.* 2009).

In this study, we evaluate the influence of landscape and management practices on pollination and fruit production in north-eastern South Africa, a region rich in well-preserved natural areas that support a diverse plant community (Shackleton 2000). The target crop, mango *Mangifera indica* L. (Anacardiaceae), is one of the most economically important fruit crops in Africa and in the tropics worldwide (FAO 2010), and relies on insects for successful fruit set (Dag & Gazit 2000). A number of commercial mango farmers in the study region rent managed honeybees (an indigenous native species) to supplement pollination. Our objectives were three:

1. To identify potential mango pollinators, their alternative food resources and assess pollinator effectiveness. A diverse community of insects including honeybees, other flying visitors and ants, visits mango crops (Anderson *et al.* 1982; Eardley & Mansell 1993); therefore, we expect all three groups will be important for mango fruit production in our study area.

2. To determine how landscape and farming management practices affect mango pollinators. Although the dispersal ability of wild flower visitors limits their abundance in agricultural fields, pollinator limitation might be less marked in highly diverse landscapes that can support diverse pollinator communities (Ghazoul 2005; Winfree *et al.* 2009). Therefore, we expect that pesticide use and distance to natural habitat will have a negative effect on wild pollinator assemblages; however, these effects will be mitigated on farms with managed honeybees and on farms in landscapes with a high proportion of intact natural habitat.

3. To test if crop production can be predicted based on pollinator abundance. The relationship between pollinator abundance and crop production can be affected by the ability to self-pollinate and by management practices such as water and nutrient addsition (Klein *et al.* 2009; Lonsdorf *et al.* 2009). Therefore, we expect that, under the same management regimes, mango production at a specific geographic location will be predictable by models based on self-pollination ability and factors that influence pollinator abundance.

Materials and methods

This study was conducted in a farming region of NE South Africa (*c.a.* 6400 ha), located between two large protected nature areas (Blyde River Canyon Nature Reserve and Kruger National Park, 24°31′S 30°44′E). Twelve mango farms were selected (2–14 km apart), four with conventional farming practices and without managed honeybees, four with conventional farming practices and with managed honeybees and four with organic farming practices and with managed honeybees. Each farm is divided into several plots, separated by windbreak lines of *Casuarina* sp. trees. Plots used in flower visitation collection and experiments were of similar size (*c.* 0·9 ha). Hive density on farms using managed honey bees was 1·1 hives ha^{-1}. On conventional farms insecticides (neonicotinoids or organophosphates) and herbicides (glycophosphates) are used, the former being applied outside of the mango flowering season. On organic farms, mango pests are controlled by fruit fly traps and kaolin (soft clay applied to the fruit), and weeds are controlled by regular mowing. In all farms used in this study, soil nutrient and water content of the different plots are measured every year and nutrient correction and irrigation measures are applied in order to standardize conditions within and among farms. Such detailed management actions makes the selected mango farms ideal to study the effect of biotic variables, such as flower visitation. Although flower visitation is expected to be similar between different mango cultivars (Anderson *et al.* 1982), data collection was restricted to only one cultivar, Kent, which was common to all farms, and widely planted due to its consistently satisfactory yields (Villiers & Joubert 2008). All statistical analyses were performed using the software R (R Development Core Team 2009).

QUESTION 1 – ARE FLOWER VISITORS EFFECTIVE POLLINATORS OF MANGO?

To identify mango flower visitors and understand how the network of interactions in which they participate changes throughout the mango flowering season, flower visitor surveys were carried out monthly from July to September 2008, on each of the 12 farms, totalling 36 surveys. As anthesis is diurnal (Siqueira *et al.* 2008), surveys were performed during warm dry days (20–39 °C) with moderate wind speed (0–4 km h^{-1}), between 8·00 and 16·00 h. On each farm, flower visitor data were recorded while walking one transect (60 × 2 × 2 m) placed within a randomly selected plot. Whenever open flowers were encountered, the observer would stop for 5-s and register all flower visitors, which were collected whenever possible for taxonomic identification. Mango is a hyperabundant flowering species, so the total number of flowers in the transect was estimated by counting the number of open flowers of three randomly selected inflorescences, the average being multiplied by the total number of inflorescences counted in the transect. Flower visitors were identified by professional taxonomists (see Acknowledgements), and food-webs were drawn using software written in MATHEMATICA© (Wolfram Research, Inc., Champaign, IL, USA). To assess how overall plant (flower resources) and flower visitor communities (abundance and species richness) varied throughout the mango flowering period, generalized linear mixed effects models (GLMM, Poisson error distribution) were used with month as a fixed factor and farm as a random factor (R package lme4).

As visitation rates to mango flowers were low (see Results), individual assessment of pollination effectiveness was impractical. Therefore, a flower visitor exclusion experiment was conducted on nine of the 12 farms (see Table S 1, Supporting information) to quantify the effect of three categories of potential pollinators, namely crawling visitors (i.e. ants), wild flying visitors (including wild honeybees) and managed honeybees. We assumed that wild honeybees were equally abundant on farms with and without managed honeybee hives, hence on the latter farms all honeybees were wild, while on the former, honeybees were both wild and managed. In June 2008 (when mango inflorescences were still immature), 10 trees were randomly selected per farm, with three treatment inflorescences each: (i) *accessible to flying and crawling visitors* – open inflorescences; (ii) *accessible to flying visitors only* – all crawling visitors were excluded by placing a ring of petroleum-based grease around the base of the inflorescence and by removing any branches or leaves providing natural bridges and (iii) *not accessible to any visitors* – all flower visitors were excluded by placing a fine mesh bag around the inflorescence, using a wire structure to avoid any contact between the bag and the flowers. Inflorescences were checked every month, to reinforce the grease rings and ensure that no new bridges had been created. Fruit set (viable and aborted considered separately) was ascertained 5 months later, when fruits were developed but still immature. To determine if fruit set varied between the flower visitation treatments, GLMM (Poisson error distribution) were used with treatment (no visitors, flying visitors only and flying and crawling visitors) and presence of managed honeybee hives (present vs. absent) as fixed factors and farm as a random factor. The contribution of crawling visitors was assessed by comparing fruit set in inflorescences with both crawling and flying visitors to that in inflorescences with only flying visitors. The contribution of flying visitors was assessed by comparing fruit set in inflorescences with only flying visitors with inflorescences with no visitors. The contribution of managed honeybees was assessed by comparing fruit set in farms with and without managed honeybee hives. Interaction effects between treatment and presence of managed honeybees were also tested.

QUESTION 2 – DO LANDSCAPE AND FARMING MANAGEMENT PRACTICES AFFECT MANGO POLLINATORS?

As flower resource availability can influence insect visitation rate (Lopezaraiza-Mikel *et al.* 2007), we used only mango flower visitor data collected during the peak mango flowering season (i.e. August, see Question 1). Abundance data were standardized between farms by dividing the number of flower visitors by the total number of flowers observed, then multiplying by the overall average number of flowers per transect. The distance from the centre of each plot to natural habitat and the percentage of natural habitat within a 1 km radius were measured based on 2008 aerial photographs using ArcGis9® (ESRI, Redland, CA, USA). Changes in landscape that occurred after the date of the photographs, but before the flower visitor surveys, were taken into account and corrected for.

To ascertain how abundance and species richness of potential pollinators varied with landscape and management measures, a model selection procedure was carried out (Generalized linear models, Poisson error distribution) using distance to natural habitat, percentage natural habitat, use of managed honeybee hives and use of pesticides as fixed variables. All possible combinations of explanatory variables and their interactions were considered. The most parsimonious model was selected as that with the lowest AICc, Akaike information criterion with a second-order correction for small sample sizes (Burnham & Anderson 2002). To check if any explanatory variables were correlated with each other we used Pearson's product-moment correlation tests. To separate the effect of introduced hives on wild honeybees, we tested for an effect of managed honeybee presence–absence on honeybee abundance in transects.

QUESTION 3 – CAN MANGO PRODUCTION BE PREDICTED BASED ON THE ABUNDANCE OF POLLINATORS?

Empirical data on relative fruit set rates for flying vs. crawling visitors (Question 1) and on changes in pollinator visitation rates (Question 2) were used to make a predictive model of fruit set. We then tested the model fit against empirical production data (kg per tree of commercially suitable mangoes) provided by farmers for Kent plots across four of the 12 farms used in this study (see Table S1, Supporting information), by testing if residuals (ratio observed–expected) differed significantly from one. All 95 plots used in this analysis were consistently productive plots of similar size (0·4–1·1 ha), age (12–15 years) and density (550–960 trees ha^{-1}). For each plot, the distance from the midpoint to natural habitat was measured as in Question 2. Finally, we compared the predictive model with a regression model of production data against factors that influenced pollinator abundance (i.e. distance to natural areas; see results Question 2). The regression model was calculated using GLMM with farm as a random factor.

To fully evaluate the constancy of the pollination service over multiple seasons, it is essential to consider the periodic variations that can affect insect communities and production (Klein *et al.* 2007). To address this issue, we repeated the analysis with production data from the previous season (2007).

Results

QUESTION 1 – ARE FLOWER VISITORS EFFECTIVE POLLINATORS OF MANGO?

Throughout the mango flowering season, 32 insect species visited mango flowers (see species details in (Tables S2 and S3), Supporting information), occasionally feeding on some of the other 29 flowering plant species found in low abundance within mango plots, (Fig. 1). Despite the high number of flowers observed throughout the 36 field surveys, flower visitation in mango fields was extremely low (167 insects observed overall). During the mango flowering season, the two most frequent mango visitors were ants (the only crawling insects found, 44%). Among flying visitors honeybees were one of the most abundant species (9% of the visits). Moreover, although alternative flower resource abundance was significantly lower before and after mango flowering peak than during the peak (July vs. August: $z = 143{\cdot}1$, $P < 0{\cdot}0001$; August vs. September: $z = 171{\cdot}1$, $P < 0{\cdot}0001$), mango flower visitor abundance and diversity significantly increased from July to August and then remained constant until September (flower visitor abundance – July vs. August: $z = 5{\cdot}6$, $P < 0{\cdot}0001$; August vs. September: $z = 1{\cdot}1$, $P > 0{\cdot}05$; flower visitor species richness – July vs. August: $z = 4{\cdot}1$, $P < 0{\cdot}0001$; August vs. September: $z = 0{\cdot}6$, $P > 0{\cdot}05$, see Fig. 1).

Several events (e.g. herbivory, diseases) led to a reduction of the initial number of inflorescences in the exclusion experiment. The final number of inflorescences used in the experiment was 78 (no visitors), 47 (flying visitors only) and 63 (ants and flying visitors). The results revealed that both ants and flying visitors contributed significantly to mango pollination

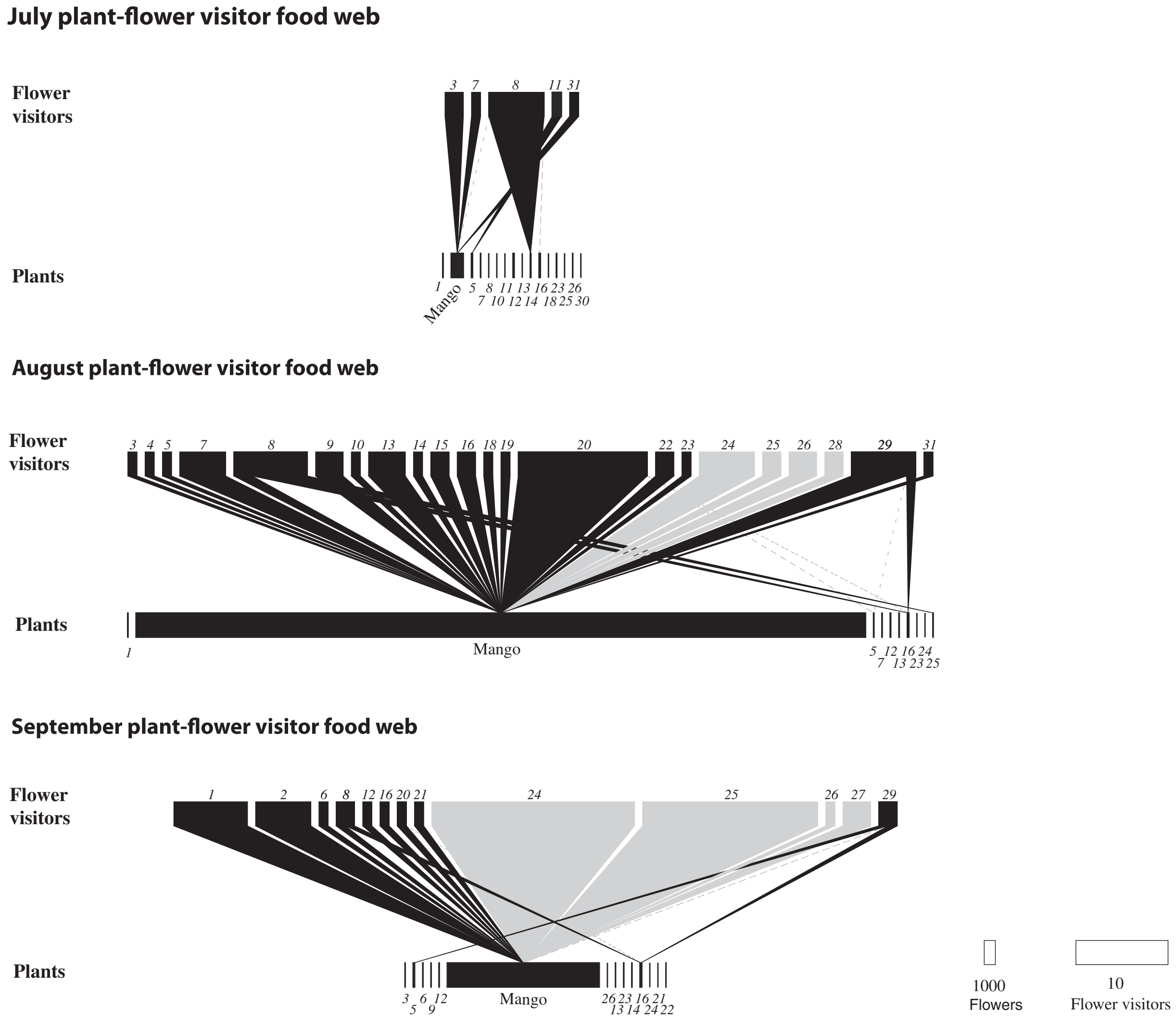

Fig. 1. Flower visitation web during 2008 mango flowering season (July to September). Each of the three food-webs results from pooling data from 12 mango farms sampled in this study. Detailed information for the 36 surveys is presented in (Fig. S 1). Each species of plant and insect is represented by a rectangle. A list of plant and visitor species is provided in the (Tables S 2 and S3). The widths of the rectangles represent overall species abundance at the field site and the size of the lines connecting them represents the frequency of interaction in the study area. Flying flower visitors are shown in black, while ants are presented in grey.

(Fig. 2, see detailed statistical results in Table 1), increasing final fruit set (only viable fruits). There was no significant interaction between treatment and presence of managed honeybee hives. No significant effect was detected in the number of aborted fruits between treatments ($z = 0{\cdot}35$, $P > 0{\cdot}05$, $n = 188$). Moreover, the presence of managed honeybee hives had no significant effect on fruit set. In summary, only two groups of flower visitors (ants and wild flying insects) contributed significantly to mango pollination.

QUESTION 2 – DO LANDSCAPE AND FARMING MANAGEMENT PRACTICES AFFECT MANGO POLLINATORS?

Although distance to natural habitat did not contribute significantly to explain the variation in the ant community (abundance and species richness), it did affect flying visitors, with abundance and species richness dropping to 17% and 11% of the maximum at 500 m respectively (Fig. 3). Neither the percentage natural habitat within a 1 km radius, nor the presence of managed honeybees contributed significantly to explain changes in the flower-visitor community (see details in Table 2). Pesticide application (organic farming practices vs. conventional farming practices) had no significant effect on any of the three groups of flower visitors. Interactions between explanatory variables made no significant contribution to the flower visitor models. Furthermore, the presence of managed honeybee hives did not affect the overall number of honeybees visiting mango flowers. None of the explanatory variables were intercorrelated.

QUESTION 3 – CAN MANGO PRODUCTION BE PREDICTED BASED ON ABUNDANCE OF POLLINATORS?

Neither the use of managed pollinators nor use of pesticides contributed significantly to models on the abundance of

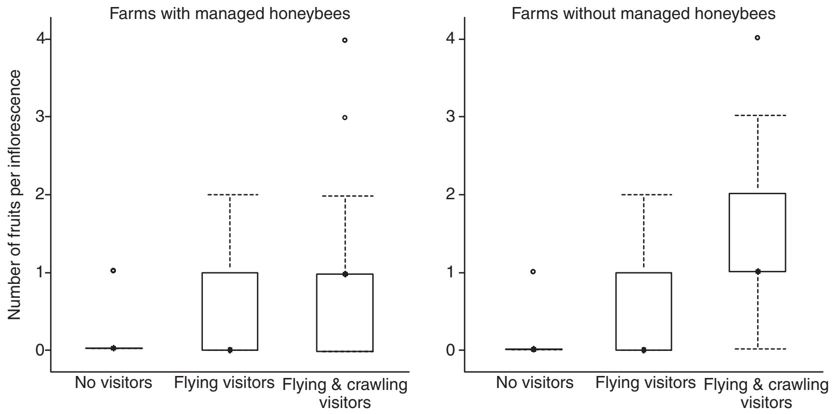

Fig. 2. Mango seed set in the three exclusion experiment treatments in farms with and without managed honeybees (see Table 1 for statistical details). Farms with managed honeybees: no visitors, $n = 51$; flying pollinators only, $n = 31$ and flying and crawling pollinators, $n = 42$. Farms without managed honeybees: no visitors, $n = 27$; flying visitors only, $n = 16$ and flying and crawling pollinators, $n = 21$. Error bars represent the upper and lower quartiles (due to the high number of inflorescences with no fruits, first and second quartile are sometimes coincident in 'flying and crawling visitors', and in 'flying visitors' and all quartiles are coincident in 'no visitors').

Table 1. Effect of flower visitors on number of fruits per inflorescence – exclusion experiment results

Response variable (Y)	Treatment (T), P value	Managed honeybees (MH). P value	Interaction $T \times$ MH, P value	AIC
Number of fruits				
Model 1 (best model)	< 0·0001	–	–	169·2
Model 2	< 0·0001	ns	–	170·2
Model 2	< 0·0001	ns	ns	173·7
Best model equations for the different levels of treatment				
Ants and flying visitors	$Y = e^{-0·35\pm0·19}$	Open inflorescences fruit set (100%)		
Flying visitors	$Y = e^{-0·91\pm0·46}$	43% drop due to the exclusion of ants visitors		
No visitors	$Y = e^{-1·92\pm0·52}$	Further 36% drop due to the exclusion of flying visitors (21% remaining due to self-pollination)		

P-value obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. 'ns', $P > 0·05$. '–', variable not included in the model. Number of observations was 188 and there were nine farms (random variable).

pollinators (Table 2); therefore, our prediction of a decline in mango production is based solely on the decline of pollinators with distance to natural habitat. Mango fruit set resulted from self-pollination (Pself-pollination) and from pollination provided by two groups of visitors that are affected differently by landscape changes, ants (Pants) and flying visitors (Pfv), see results of Question 2. The contribution of each of these modes of pollination was considered separately in the model:

$$P_i = \text{Pself-pollination}i + \text{Pants}i + \text{Pfv}i, \quad \text{eqn 1}$$

where Pi is production at i metres from natural habitat. Based on the statistically estimated parameters presented in (Tables 1 and 2), our final predictive model for mango production as a function of distance from natural habitat was:

$$P_i = \text{Pmed}_{(i=0)} \times (0 \cdot 64 + 0 \cdot 36 \times e^{-0·0035 \times i}), \quad \text{eqn 2}$$

where Pi is production at i metres from natural habitat and Pmed is the median mango production under the selected management rules (see details of model construction in Appendix S1, Supporting information). This model predicts that median production can drop 30% at 500 m from natural habitat (when $i = 0$, P_i = Pmed; when $i = 500$, $P_i = 0·7 \times$ Pmed). The model provides a good fit to 2007 empirical production data (residuals were not significantly different from one), but a poor fit to the 2008 data, significantly overestimating production at greater distances from natural habitat (t-value = 3·4; $P < 0·02$).

Although there was considerable variation in real production data within farms, particularly in areas close to natural habitat, there was a clear decline in the maximum production obtained over distance from natural habitat (Fig 4). The equations from the regression model derived from real production (Poisson error distribution) were:

$$\text{2007 Production} \rightarrow P_i = e^{2·8628-0·001 \times i}, \quad \text{eqn 3}$$

$$\text{2008Production} \rightarrow P_i = e^{3·2413-0·001 \times i}, \quad \text{eqn 4}$$

Real production declines (eqns 3 and 4) were greater than that predicted by the model derived from flower visitation data

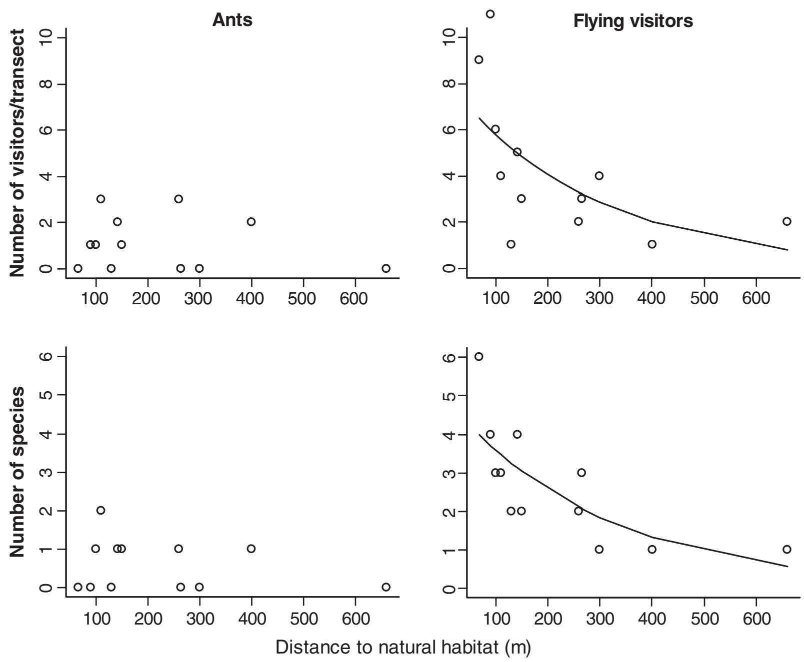

Fig. 3. Effect of distance to natural habitat on the abundance and species richness of the two main types of mango pollinators (ants and flying visitors). Regression lines are presented whenever a significant value was detected (see Table 2 for statistical details).

(eqn 2), with median production dropping 39% and 42% in the 2007 and 2008 fruit seasons respectively.

Discussion

The susceptibility of biodiversity-rich regions to the recently debated pollination crisis is still unclear (Ghazoul 2005). Our study provides one of the first examples of a clear link between landscape transformation (natural habitat being transformed into a continuous crop system) and crop production in a subtropical biodiversity-rich area where natural habitat still forms the landscape matrix (see also Klein, Steffan-Dewenter & Tscharntke 2003; Blanche, Ludwig & Cunningham 2006). Use of healthy managed pollinators did not mitigate the negative effects of isolation from natural habitat on crop pollination. In this section, we discuss the results obtained in view of our original predictions while considering the limitations of the study, and highlight the implications of our results for agriculture and conservation.

QUESTION 1 – ARE FLOWER VISITORS EFFECTIVE POLLINATORS OF MANGO?

In agreement with previous studies (e.g. Anderson *et al.* 1982), mango were visited by a highly diverse community of pollinators. The low number of visits recorded is likely to be related to the scarcity of resources outside the mango flowering peak season (Fig. 1), probably caused by the frequent mowing to which all farms used in this study are subjected, and to the low attractiveness of mango flowers to local flowers visitors (Free & Williams 1976). Nevertheless, the high abundance of resources during August (mango flowering peak) may have led flower visitor species to select breeding places nearby (Suzuki *et al.* 2009), explaining the higher than expected abundance and diversity of visitors in September. Therefore, it is possible that an increase in the abundance of flower resources within farms, particularly species flowering before mango, would have a positive impact on mango flower visitation.

Ants (the only crawling visitors) and wild flying visitors were both effective pollinators of mango, with ants making a higher contribution than flying visitors to pollination (Table 1). Ants can be effective pollinators of several plant species (Carvalheiro, Barbosa & Memmott 2008a). In Australia (Anderson *et al.* 1982), Jamaica and Kenya (Free & Williams 1976), ants were also identified as abundant and efficient mango flower visitors. Although ants have limited mobility and hence limited capacity to promote gene flow, there were no significant differences in the number of aborted fruits between any of the treatments. This suggests that the quality of pollen transported by ants and flying insects was similar, i.e. that cross-pollination is not essential for mango pollination. Further studies involving pollen supplementation experiments would help clarify the importance of cross-pollination for mango production. Contrary to our predictions, the intensive use of managed honeybees did not increase fruit set (Fig. 2). Although mango flowers are not very attractive to honeybees (Free & Williams 1976) and flower visitation was generally low, honeybees were one of the most abundant flying flower visitors (Table S3, Supporting information). It is possible that only wild honeybees were visiting mango flowers while managed honeybees, which might suffer higher resource stress, avoid visits to low reward flowers (mango). The possibility of managed honeybees competing with wild flower visitors with a net zero effect change in flower visitor abundance is unlikely, because flower visitation was very low compared with the overall mango flower resource (Fig. 1) and there were no significant differences in honeybee abundance between farms with and without managed hives.

Table 2. Effect of landscape and management measures on mango pollinators

Response variable (Y)	Distance (D), P value	Natural habitat percentage, P value	Managed honeybees, P value	Pesticide use, P value	d.f.	AICc
Flying visitor abundance						
Model 1 (best model)	< 0·008	–	–	–	10	56·0
Model 2	< 0·02	ns	–	–	9	57·6
Model 3	< 0·01	–	ns	–	9	58·5
Model 4	–	ns	–	–	10	63·0
Model 5	–	–	–	ns	10	64·2
Model 6		–	ns	–	10	64·2
Best model equation $Y = e^{2\cdot1086-(0\cdot0035)\times D}$						
Flying visitor species richness						
Model 1 (best model)	< 0·05	–	–	–	10	41·7
Model 2	< 0·04	–	ns	–	9	43·8
Model 3	< 0·05	ns	–	–	9	45·3
Model 4	–	–	ns	–	10	46·3
Model 5	–	–	–	ns	10	47·2
Model 6	–	ns	–	–	10	47·3
Best model equation $Y = e^{1\cdot6061-(0\cdot0045)\times D}$						
Ant abundance						
Model 1 (best model)	–	ns	–	–	10	35·3
Model 2	–	–	ns	–	10	36·9
Model 3	–	–	–	ns	10	37·0
Model 4	ns	ns	–	–	9	38·2
Model 5	ns	–	–	–	10	38·7
Model 6	ns	–	ns	–	9	39·7
Ant species richness						
Model 1 (best model)	–	ns	–	–	10	25·4
Model 2	–	–	ns	–	10	26·6
Model 3	–	–	–	ns	10	26·9
Model 4	ns	–	–	–	10	27·4
Model 5	ns	ns	–	–	9	28·6
Model 6	ns	–	ns	–	9	29·7

Results of the six most parsimonious models are presented for each response variable, and when the variables included in the best model (lowest AICc) contributed significantly to the fit of the model, the equation is provided for each subset. P-value obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. 'ns', $P > 0{\cdot}05$. '–',variable not included in the model.

QUESTION 2 – DO LANDSCAPE AND FARMING MANAGEMENT PRACTICES AFFECT MANGO POLLINATORS?

Although pollinator abundance was low overall, it was sufficient to detect negative effects of distance to natural habitat. Abundance and species richness of flying visitors dropped by more than 80% of their maximum values over a distance of 500 m, while ants were not affected (Fig. 3). The declines in flying visitors were far more severe than the average relationship between isolation and flower visitor abundance worldwide, and for tropical regions (50% decline of visitation rate at 589 m, see Ricketts *et al.* 2008), suggesting that mango flying visitors are particularly susceptible to extensive habitat changes. Such high susceptibility may also result from the low attractiveness of mango flowers to local flower visitors, and it is possible that this effect would not be as marked in mango's native range.

The lack of effect of managed honeybees on pollinator abundance and on the overall honeybee abundance supports the exclusion experiment finding that managed honeybees are not important for mango pollination. Contrary to our expectations, neither the size of the surrounding natural areas nor the presence of managed honeybees ameliorated the negative effect of distance to natural habitat on flower visitor abundances (Table 2). It is thus clear that farmers in biodiversity-rich regions can also be affected by pollinator declines, if their fields are too large. The high variation in pollinator abundance observed near natural habitat (Fig. 3) could be attributable to differences in the assemblage of native plants present in natural areas, as certain native plants may provide more adequate floral resources or better nesting conditions than others (Suzuki *et al.* 2009).

Contrary to our initial expectations, organic farming practices did not lead to higher abundance or diversity of flower visitors (Table 2). Although the lack of pesticide application makes pollinator nesting conditions more favourable (Osborne, Williams & Corbet 1991), the absence of wild flower resources within crop fields (Fig. 1) may limit pollinators, as in-field flowers provide important food resources outside of

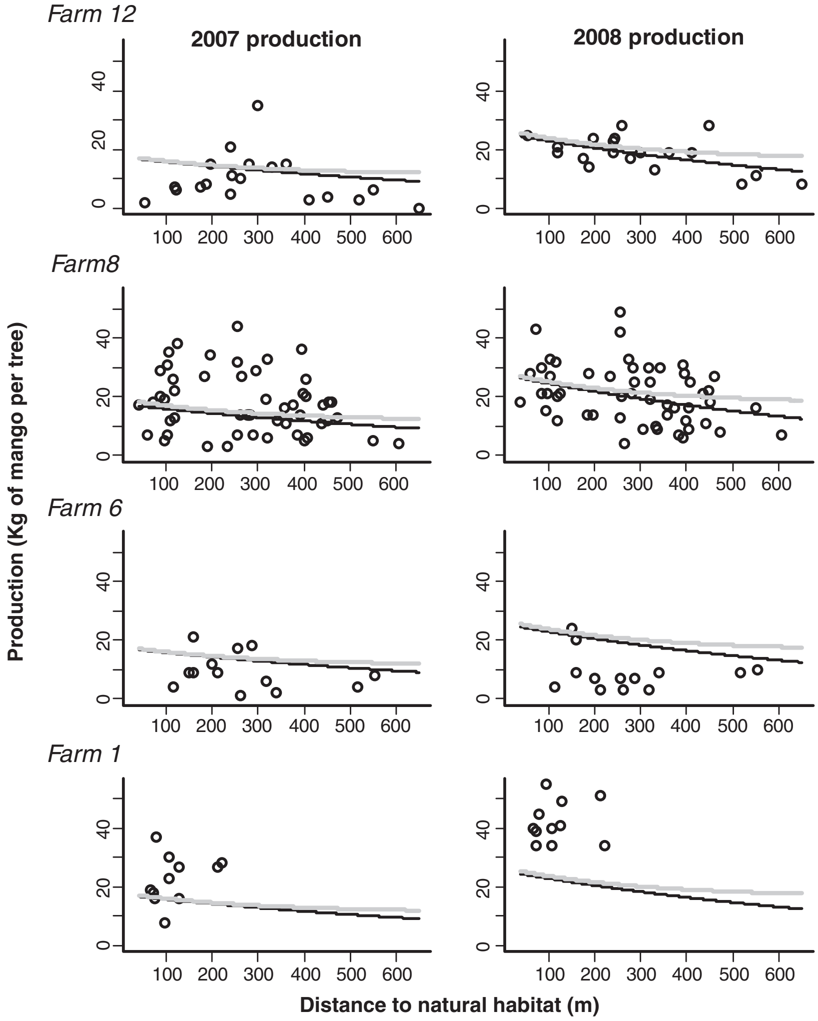

Fig. 4. Effect of distance to natural habitat on production. Black line – regression models based on empirical production data for all the farms; grey line – predictive model based on pollinator abundance. For each year: 95 production data points; four random variable (farm) groups.

the mango flowering season. Experiments involving the increase of native flower resources within farms would help clarify these results and the positive effects of such an experiment would then be more likely to emerge in farms with organic management practices. This is nonetheless consistent with previous studies that have found organic management to be a weaker driver of bee abundance than landscape context (e.g. Winfree *et al.* 2007).

QUESTION 3 – CAN MANGO PRODUCTION BE PREDICTED BASED ON ABUNDANCE OF POLLINATORS?

Our results suggest that maintaining natural habitat areas within farmland could increase crop flower visitation; however, this may conflict with the common strategy of expanding orchard areas to increase production. Thus, it is vital to understand the extent to which the declines in pollinators observed here affect production. Our study shows that increasing isolation from natural habitat led to strong declines in production (~40% less production at 500 m). As mango farmers in the study region regularly control and standardize soil abiotic conditions (water and nutrient content), this result suggests that pollinator abundance is an important driver of mango production. However, models based solely on pollinator abundance decline underestimated production declines (Fig. 4) suggesting that other factors may interfere with mango production. Recent studies reveal that the pollination effectiveness of flying visitor species can be increased in the presence of a higher diversity of flower visitor species, as inter-specific interactions may promote flying visitor movement between flowers (e.g. Greenleaf & Kremen 2006). As species richness of flying flower visitors also declined significantly with distance to natural habitat (Fig. 3) it is possible that the loss of diversity acted synergistically with the negative effects of declines in pollinator abundance. However, such an effect would only occur if cross-pollination lead to a higher fruit set than pollination within the same plant and the high contribution of ants (with very limited foraging ability) towards fruit set suggests that cross-pollination is not essential. More detailed analysis where production data could be analysed directly against empirical data on species richness vs. abundance of pollinators would be necessary to evaluate such synergistic effects.

MANAGEMENT RECOMMENDATIONS FOR FARMERS

Because managed honeybees are not suitable mango pollinators and as more efficient wild pollinators cannot access isolated areas of orchards, we conclude that mango crops are highly vulnerable to isolation from natural habitat. Our findings concur with the fact that despite modern agriculture methods to increase production, the percentage increases in production of the last 40 years of several pollinator-dependent crops were considerably lower than the percentage increases in plantation area (Garibaldi *et al.* 2009), including mango (see supplementary material of Aizen *et al.* 2008).

Although different crops will vary in their pollination requirements, our results enable us to identify some simple management recommendations that may benefit insect communities, with concomitant improvement in pollinator-dependent crop production. For example, exchanging investment in creation of further contiguous agricultural areas and renting of managed honeybees with investment in creating pollinator-friendly corridors may be more profitable for pollinator-dependent crops (see also Keitt 2009). These corridors would require preservation of the remaining natural habitat fragments on farms, as well as restoration of native flower patches, in areas within agricultural landscape. Although successful habitat restoration can be challenging, these areas may provide essential flower resources throughout the seasons (Tuell *et al.* 2008), benefiting flower visitors (Albrecht *et al.* 2007; Holzschuh, Steffan-Dewenter & Tscharntke 2010). Production losses due to the replacement of farmland by wild vegetation corridors can be perceived by farmers as more costly than the loss of pollinators itself (Ghazoul 2007). Therefore, it is essential to promote further studies that quantify production losses per hectare due to pollinator declines and to ensure that such information reaches the farmers. Furthermore, as not all weeds will compete with crop species, and some are probably beneficial to pollinators (Gemmil-Herren & Ochieng 2008), allowing weeds to co-exist with mango trees may increase the provision of flower resources to pollinators as well as avoid the disturbance caused by frequent mowing, which can negatively impact pollinator nesting sites. Adopting such management practices could also make organic farming far more profitable than at present.

IMPLICATIONS FOR CONSERVATION

One of the most important current challenges for conservation is the maintenance of food and energy supply to the continuously growing human population, whilst minimizing the destruction of natural habitat. The results of this study further illustrate the extent to which agriculture and natural habitat are ecologically connected, and that the maintenance of ecosystem services from wild nature is essential to sustainable farming. By ensuring maintenance of diverse pollinator communities within farmlands, agro-environmental practices such as those we suggest may also benefit nature conservation, promoting the diversity of pollinator assemblages for native flora, and hence, plant species diversity in the natural surrounding areas (e.g. Fontaine *et al.* 2006; Klein *et al.* 2009). Moreover, as flower visitors are an important component of the diet of many predator/parasitoid species the negative impacts reported here for insect communities can easily propagate through food-webs, affecting the more susceptible higher trophic levels (e.g. Carvalheiro *et al.* 2008b).

Concerns that the use of economic arguments for preserving nature will weaken non-economic justifications and encourage manipulation of ecosystem services are growing (Redford & Adams 2009). However, it is becoming increasingly evident that to ensure pollinator-dependent crop production through time, preservation of a diverse community of wild species is required (Winfree *et al.* 2007; Winfree & Kremen 2009). Moreover, the uncertainty of future community floral/pollinator species composition makes it essential to preserve flower visitor communities holistically, as well as the complex network of interactions on which they rely, to guarantee availability of pollination services.

IMPLICATIONS FOR PREDICTIVE STUDIES

Outlining general guidelines for management of pollinators as an ecosystem service is an important step for maximizing the delicate balance between conservation and agricultural expansion. Although still rare, spatially explicit analyses of production, pollinator communities and landscape data, such as this study, are essential to improve our understanding of how landscape influences pollinator services (Kremen *et al.* 2007). Recent studies have developed spatially explicit models that aim to predict pollinator abundance, and ultimately from this, pollination services available on farm sites (Lonsdorf *et al.* 2009). Although these models assume a close correlation between pollinator abundance and pollination effectiveness (see Vázquez, Morris & Jordano 2005), the economic dependence of farming on pollinators remains unclear. Our results give strength to these assumptions as it becomes clear that pollinator abundance is an important driver of commercially suitable fruit set of our study crop. However, the high unexplained variation in production values in areas near natural habitat suggest that models which aim to accurately predict pollination services might have to consider other biotic factors that affect flower visitor abundances (e.g. local floral composition in the surrounding habitat). Furthermore, the underestimation of pollination service suggests that other factors influencing pollination effectiveness (e.g. flower visitor diversity) may also need to be taken into account.

Conclusion

Until recently, perceptions of a pollinator crisis were driven mainly by reported declines of crop-pollinating insects in North America and in Europe (Ghazoul 2005). Here, we found that even in tropical/subtropical areas, where natural habitat is well represented, the presence of a diverse, healthy and abundant assemblage of crop pollinators cannot be assumed even at distances as close as 500 m to natural habitats. Maintaining healthy and abundant communities of wild pollinators within farmland presents a challenge to both farmers and conservationists. As farmland expansion is unlikely to slow in the foreseeable future, conserving pollinator-supporting habitats within farmlands can clearly bring benefits to both agriculture and conservation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Production model details.

Table S1. Summary details of the mango farms used in this study

Table S2. List of flowering plants recorded during mango flowering season

Table S3. List of flower visitors recorded during mango flowering season

Figure S1. Plant–flower visitor food-webs for the 12 farms

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