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Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study

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Summary

1. As cropland increases, fields become progressively isolated from pollinators, leading to declines in pollinator-dependent crop productivity. With the rise in demand for pollinator-dependent foods, such productivity losses may accelerate conversion of natural areas to cropland. Pollination–compensation measures involving managed pollinators or hand pollination are not always optimal or are too costly. Introducing areas of native vegetation within cropland has been proposed as a way to supplement crop pollinators, but this measure is perceived by farmers to carry costs outweighing benefits to agricultural production. Studies quantifying benefits of small patches of native flowers to crop pollination are therefore necessary to encourage such practices.

2. To ascertain whether provision of floral resources within farmlands can facilitate pollination, and hence, crop yields, small experimental patches of perennial native plants (native flower compensation areas, NFCAs) were created in nonproductive areas of large commercial fields of several cultivars of mango *Mangifera indica*.

3. Pesticide use and isolation from natural habitat were associated with declines in flying visitors and in mango production (kg of marketable fresh fruit), but presence of NFCAs ameliorated these declines, and NFCAs did not harbour any mango pests. In areas far from natural vegetation, orchards near NFCAs had significantly higher diversity and abundance of mango flying visitors, as well as mango production, than orchards far from NFCAs, although these measures were still lower than in orchards close to natural areas.

4. Neither the most abundant flower visitors to mango (ants) nor initial fruit set was significantly affected by distance, pesticides or NFCAs, suggesting that although fertilization is associated with factors unaffected by isolation from natural habitat and pesticide use (i.e. self- and ant-pollination), viable fruit set (and ultimately, production) requires cross-pollination, for which flying visitors are essential.

5. *Synthesis and applications*. Our results show that the presence of small patches of native flowers within large farms can increase pollinator-dependent crop production if combined with preservation of remaining fragments of natural habitat and judicious use of pesticides. Native flower compensation areas represent a profitable management measure for farmers, increasing cost-effectiveness of cropland while indirectly contributing to preservation of natural habitat.

Key-words: agro-ecosystems, ants, bees, crop yield, ecological compensation areas, ecosystem services, facilitation, flower diversity, managed honeybees, pollination

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Introduction

Pollinator-dependent products form an essential part of human diets (Eilers *et al.* 2011). Although modern farming practices have enabled overall higher crop productivity (Aizen *et al.* 2008, 2009), declines in pollinator-dependent crop yields have been observed, often owing to isolation from natural habitat (Klein, Steffan-Dewenter & Tscharntke 2003a; Garibaldi *et al.* 2011). In view of the increasing demand for animal-pollinated crops in human diets (Garibaldi *et al.* 2009), such productivity losses can accelerate conversion of natural areas to cropland.

Farmers attempt to compensate for the effects of reduced pollinator abundance using managed pollinators or, rarely, hand pollination (Garibaldi *et al.* 2009). For many crop species, however, managed pollinators are unsuitable (e.g. Kevan 1999) or insufficient when acting alone (Greenleaf & Kremen 2006; Carvalheiro *et al.* 2010; Breeze *et al.* 2011). Furthermore, hand pollination is seldom economically viable (Allsopp, de Lange & Veldtman 2008). Maintenance or creation of native flower compensation areas (hereafter NFCAs), containing a diverse assemblage of flowering plants within farmland, could increase provision of wild pollination services (Winfree *et al.* 2008; Carvalheiro *et al.* 2011). Yet, without financial incentives, this practice is seldom adopted because it remains unclear whether NFCAs within farmlands are sufficient to increase crop pollinator diversity and abundance (Holzschuh, Steffan-Dewenter & Tscharntke 2010), whether other plants will compete with crops for resources or harbour crop pests, and so whether the benefits outweigh the costs (Ghazoul 2007).

In a recent study, we found that pollination of one of the main cultivars (Kent) of mango *Mangifera indica* L. (Anacardiaceae) in South Africa is highly dependent on a diverse assemblage of flying visitors, which is strongly negatively affected by distance to natural habitat (Carvalheiro *et al.* 2010). We therefore set out to establish whether creation of small NFCAs within nonproductive crop areas (orchard margins), can increase crop flower visitor abundance and diversity, and whether this improves crop yield (kg of mangoes per tree). Little is known of how the importance of pollinators varies between cultivars (but see Free & Williams, 1976). Here, we evaluated flower visitation and production of the three most important cultivars planted in the region: Kent, Keitt and Tommy Atkins.

Mango flowers are unspecialised, enabling pollination by most insects (Heard 1999). These pollinators are critical for successful fruit set of mango flowers (Free & Williams, 1976, Anderson 1982, Richards 2001; Carvalheiro *et al.* 2010) and are sensitive to isolation from natural habitat, but sometimes also to pesticides (De Siqueira *et al.* 2008). We therefore expected isolation from natural habitat to be the main cause of flower visitor losses within mango fields. As floral diversity can positively influence diversity of flower visitors (Klein, Steffan-Dewenter & Tscharntke 2003b; Ebeling *et al.* 2008; Winfree *et al.* 2008; Carvalheiro *et al.* 2011), we anticipated that NFCAs might ameliorate negative effects of isolation from natural habitat on flower visitors and mango production.

Materials and methods

The field data for this study was collected in 2009 (May–September) in four large mango farms within the same area as our 2008 study (Carvalheiro *et al.* 2010) in NE South Africa, which included orchards managed with conventional and organic farming practices. All orchards selected for this study within these farming regions were similar in size, tree age and density, and were subjected to similar management practices (for further details of location and management practices see Fig. S1, Supporting information). During mango flowering, all farms studied have managed honeybee *Apis mellifera scutellata* Lepeletier colonies (at least one hive per ha), although previous studies in Africa have found that honeybees are not very attracted to mango flowers (Free and Williams 1976; Carvalheiro *et al.* 2010). On all farms used in this study, soil nutrient and water content of the different orchards are monitored annually, and correction measures implemented to standardize conditions to those considered optimal for mango production (J. du Preez and H. Groove pers. comm.). These uniform management strategies minimize abiotic variability between sites, facilitating comparison of biotic variables.

In each of the four farms, an NFCAs was created at least 250 m away from natural habitat (a distance at which we expect less than half of the potential maximum abundance and diversity of visitors, see Carvalheiro *et al.* 2010). NFCAs were *ca.* 25 m^2 in size, located in a corner of four mango orchards, and positioned so as not to interfere with normal management practices. Although ideally these NFCAs should comprise a diverse set of native plant species, we limited ourselves to two perennial native species that are present within the regional natural vegetation, flower before and during mango flowering season and have different floral structures. We used *Aloe greatheadii* Schönland (Asphodelaceae), which is attractive to many insects (Human & Nicolson 2006) and *Barleria obtusa* Nees (Acanthaceae), visited by flies and bees (Potgieter & Edwards 2005). We planted 30 individuals of each species, arranged alternately, in each NFCA. Flower visitation and production of orchards of the three cultivars located near NFCAs was recorded (see survey methods below). Although no mango pests were found in these plant species during preliminary surveys (see Table S1, Supporting information), 30 fruits from each plant species were collected within each NFCA (totalling 120 fruits per species) and kept under laboratory conditions to capture any insects emerging over a period of 6 months.

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO FLOWER VISITOR COMMUNITIES

Visitation surveys were conducted for both mango and the two planted species within the four NFCAs on warm, still, dry days (temperatures between 20 and 39 °C, wind speed <4 km h^{-1}) between 08:00 and 16:00.

Timed focal point observations (2 × 10 min per plant species) were conducted in each NFCA, every month before and during the peak mango flowering season (i.e. from June until September), totalling 320 min of observation per species. In each 10-min observation period, the recorder observed all open flowers within a semi-circle of *c.* 50 cm (3–20 flowers for *A. greatheadii* and 2–10 flowers for *B. obtusa*). All flower visitors observed were recorded and collected for identification.

Mango flower visitation surveys were carried out in 21 orchards that were far from NFCAs (i.e. at least 250 m away) and in 11 orchards near NFCAs (i.e. orchards with centres 50–150 m from NFCAs). Fourteen orchards (of which five were near NFCAs) were organic and 18 (of which six were near NFCAs) conventional (see Table S2, Supporting information). To standardize conditions with respect to flower abundance, only orchards with more than 75% of inflorescences in flower were surveyed, yielding 62 surveys. Mango surveys were conducted only during peak mango flowering season (August and September 2009; two surveys per orchard about 4 weeks apart), in the centre of the orchard, along a 60×2 m transect comprised of two linear 30-m sections parallel to mango rows. In orchards near NFCAs, distance between the start of the transect and NFCAs was *c.* 40–120 m (depending on orchard size). Transects were walked slowly for 10–15 min; when insect activity was encountered, the observer would observe for a minimum of 5 s, recording all flower visitors that contacted the stigma or anthers. Immediately after observation, flower visitors were collected whenever possible for later identification. The total number of flowers in the transect was estimated by counting the number of open flowers of three randomly chosen inflorescences, averaging this value and then multiplying this by the total number of inflorescences in the transect. Flower visitor abundance data were divided by the total number of flowers observed, then multiplied by the overall average number of flowers per transect. As flower visitation rates to mango are low in this study area (Carvalheiro *et al.* 2010), and rare interactions might easily be missed by this survey method, species richness surveys were complemented with three 5-min collection surveys conducted simultaneously next to the transect by a second observer, using three randomly chosen mango inflorescences in which the observer captured all flower visitors observed. Any new interactions detected during this observation period were included in the data set as rare interactions (frequency of occurrence = 0·01). All flower visitors were collected and sorted to morphospecies and subsequently sent to professional taxonomists (see Acknowledgements) for identification.

As *A. greatheadii* is very attractive to honeybees (see Results), and orchards have a high density of managed honeybees, we divided mango flower visitors into three subgroups for data analysis: ants, honeybees, and other flying visitors. Distances from the centre of each orchard to natural habitat were measured using maps based on aerial photographs taken in 2008 (corrected for later landscape changes), using ARCGIS 9.3® (2008; Environmental Systems Research Institute, Redlands, CA, USA).

To test whether spatial structure contributed significantly to the data variability, for all response variables, (log transformed to normalize residuals) we compared a null model with a model that includes a residual spatial correlation structure (linear and exponential variograms were considered, see Pinheiro & Bates 2000). No spatial autocorrelation was detected (see Table S3, Supporting information), and so, model selection procedures were carried out using generalized linear mixed models (GLMM) to assess how mango flower visitor abundance (honeybees and other visitors) and species richness (Poisson error distribution corrected for overdispersion when necessary, R package lme4) and the proportion of honeybees (Gaussian error distribution, with logit transformation) are affected by landscape context, management practices and NFCAs, using distance to natural habitat, use of pesticides (organic vs. conventional) and cultivar as fixed variables, and survey date within orchard as random variable. All possible combinations of explanatory variables and their interactions were considered. The most parsimonious model was selected as that with the lowest Bayesian information criterion (BIC). Whenever differences in BIC were not clear (<2 unit difference), we used the Akaike information criterion (AIC) with a second-order correction for small sample sizes, AICc (Burnham & Anderson 2002).

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO PRODUCTION

To ascertain whether changes in the flower visitor community translate into changes in mango production, we gathered data on early fruit set (i.e. number of unripe fruits per tree, *c.* 6 weeks after the end of flowering ceased) for all 32 orchards used for flower visitor surveys. Within each orchard, thirty trees were randomly selected and all developing fruits counted. As carrying capacity might be limited (Bos *et al.* 2007), and fruit abortion might reflect pollination quality (Papadakis, Protopapadak & Therio 2009), early fruit set is only an indication of pollination efficiency but may not be a good indicator of pollination quality and, hence, of final crop production and economic value. Therefore, we also obtained information on final production (kg of commercially suitable mangoes as either fresh fruit or as processed products per tree) directly from farmers, for 225 orchards far from NFCAs (i.e. at least 250 m away) and 19 orchards near NFCAs (i.e. 50–150 m from NFCAs), which included the orchards used for flower and early fruit set surveys.

As with flower visitation data, we first evaluated spatial autocorrelation of all response variables (log transformed to normalize residuals and analysed with Gaussian error distribution). When spatial structure of the data contributed significantly to explain variation (i.e. lowered AIC values, Table S3, Supporting information), the residual spatial correlation structure was maintained in all subsequent analyses (using nlme R package, Pinheiro *et al.* 2012). We assessed effects of distance to natural habitat, pesticide use (presence/absence), cultivar and NFCAs on early fruit set and final production, by testing all possible combinations of variables and their interactions and selecting that which yielded the most parsimonious model (i.e. lowest BIC, AICc). For the vast majority of orchards (231 of 244) for which farmers provided final production information, we did not have information on flower visitation, so we could not directly test the influence of visitation on production. As an additional control, to confirm if production of orchards located near NFCAs was similar to all other orchards prior to NFCA creation, we repeated the analyses with data from the same orchards from the previous year (2008), when no NFCAs were present, and hence, no effect was expected. Costs and gains of NFCAs were evaluated based on 2009/2010 costs of material, labour, and mango commercial value.

All statistical analyses were performed using R (R Development Core Team 2010).

Results

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO FLOWER VISITOR COMMUNITIES

Both *B. obtusa* and *A. greatheadii* flowered throughout the mango flowering season (Fig. S2, Supporting information). Eighteen species (bees, wasps, flies, butterflies and ants) of flower visitor were detected on *A. greatheadii* and *B. obstusa*. Bees were the most abundant visitors: 56% of visitors to *A. greatheadii* were honeybees, 37% were other bees; for *B. obtusa*, 5% were honeybees, 45% were other bees. In mango flowers, at least 56 visitor species were found, of which eight were ants (see Table S4, Supporting information). Sampling effort for flower visitors to *B. obtusa* and *A. greatheadii* was much lower than for mango (see Materials and methods) and therefore comparisons of visitor number or diversity cannot be directly made between NFCA plants and mango, without applying a correction for sampling effort. However, at least five species of flying visitors (bees and flies) foraged in both mango and NFCA plants (see Table S4, Supporting information).

Flying visitors were negatively affected by distance to natural habitat (Figs 1 and 2). However, presence of NFCAs significantly increased both species richness and abundance of mango flying visitors in orchards far from natural habitat (Table 1, see black circles in Figs 1 and 2). In orchards without NFCAs, diversity declined with isolation from natural habitat for all cultivars, being on average 47% lower at 300 m from natural habitat, (i.e. on average *c.* 2 species were lost) than near natural habitat. In orchards with NFCAs, diversity was only 7% lower. For mango non*Apis* visitor abundance, however, the effects were less clear, a model with (model 1 in Table 1) and without (model 2) NFCAs did not differ by more than 2 units in BIC or AICc values. Log-likelihood test with and without NFCAs do, however, reveal a significant effect on mango visitor abundance, which dropped 74% (farms with pesticides: *c.* 1·7 visitors lost) far from NFCAs but only 24% when NFCAs were present (see equation details in Table 1). A negative effect was detected for pesticide use, on both abundance (41% decline) and diversity (40% decline) of mango flying visitors for all cultivars.

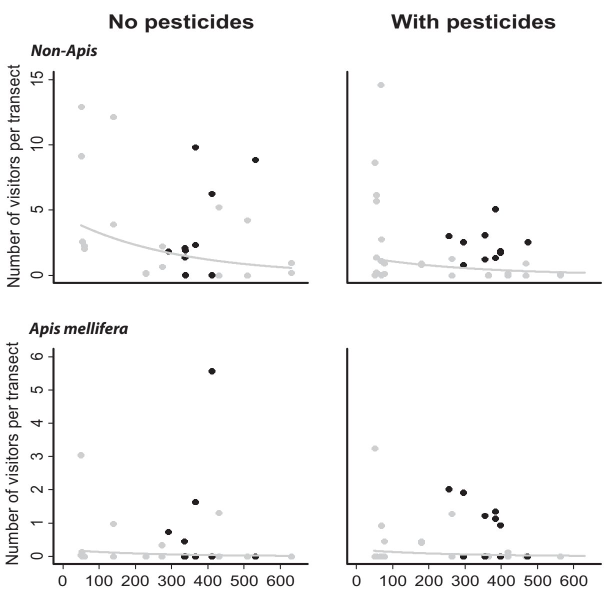

Fig. 1. Effect of distance to natural habitat, pesticide use and native flower compensation areas (NFCAs) on the abundance of flying visitors (found per transect, 60 × 2 m): non*Apis* and *Apis mellifera*. Grey circles represent orchards far from NFCAs (centre more than 250 m), black circles represent orchards near NFCAs (centre at 50–150 m), regression lines represent the effect for orchards far from NFCAs (see Table 1 for statistical details).

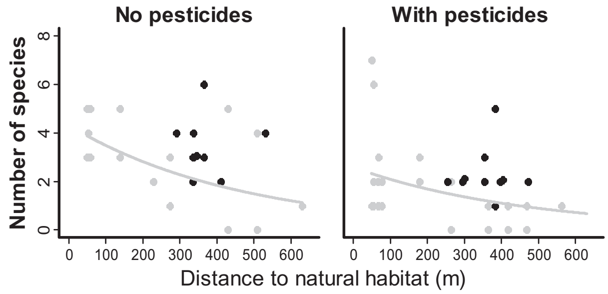

Fig. 2. Effect of distance to natural habitat, pesticide use and native flower compensation areas (NFCAs) on flying visitor species richness (found per transect, 60 × 2 m). Grey circles represent orchards far from NFCAs (centre more than 250 m), black circles represent orchards near NFCAs (centre at 50–150 m), regression lines represent the effect for orchards far from NFCAs (see Table 1 for statistical details).

Mango visitation by honeybees (both managed and wild honeybees) was also enhanced by NFCAs presence. While honeybee visits to mango were not affected by pesticides and not clearly affected by isolation from natural habitat ($P = 0{\cdot}067$, see Fig. 1), they more than doubled near NFCAs (average number of honeybees visiting mango near natural habitat = 0·2 per transect; near NFCA = 0·5 per transect, see Table 1), the proportion of honeybees among mango flower visitors increasing significantly (honeybee relative abundance: without NFCAs = 5%, with NFCAs = 18%; L.Ratio = 5·6; P-value = 0·018). Ant abundance and diversity were not significantly affected by distance to natural habitat or pesticides (Fig. S4, Supporting information). No spatial autocorrelation was detected in any of the flower visitation response variables (see Table S3, Supporting information).

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO PRODUCTION

Mango tree density and orchard size did not have a significant influence on, nor was any spatial autocorrelation detected for, initial fruit set of the selected orchards. Although early fruit set of cultivars Kent and Keitt tended to decline with distance from natural habitat (Fig. S3, Supporting information), the effect was not significant, nor was there a significant effect of pesticide use or presence of NFCAs. However, mangoes had a high rate of fruit drop/abortion (80–100% per inflorescence, L. G. Carvalheiro, pers. obser, see also Sousa, Pigozzo & Viana 2010), and final production of both Kent and Keitt showed significant declines with distance from natural habitat (Fig. 3). This effect was particularly marked for Kent, with production at only 41% of its maximum at

Table 1. Effect of distance to natural areas (DN), pesticide use (P) and NFCAs on flower visitation of all mango cultivars (C)

Response variable (Y)	DN P-value	P P-value	C P-value	NFCA P-value	NFCA*P P-value	AICc	BIC	ΔAICc	ΔBIC
Non Apis flying visitor abundance									
Model 1 (best model)	0·0002	0·0107	–	0·0077	–	142·9	157·0		
Model 2	0·0002	0·0107	–	–	–	144·7	156·8	1·8	0·2
Best model equations						Decline at 300 m from natural habitat Without NFCA			Decline at 300 m from natural habitat With NFCAs
With pesticides			$Y = e^{0.8571-0.0045 \times DN\,[+1.0812*NFCA]}$			→ 74% fewer (i.e. 1·7 visitors)			→ 24% fewer (i.e. 0·6 visitors)
No pesticide			$Y = e^{1.7374-0.0069 \times DN\,[+1.0812*NFCA]}$			→ 41% fewer visitors in orchards with pesticide			
Apis mellifera abundance									
Model 1 (best model)	0·0670	–	–	0·0009	–	66·2	78·3		
Model 2	–	–	–	0·0057	–	67·6	77·5	1·4	1·8
Best model equation			$Y = e^{-1.6151-0.0043 \times DN\,[+2.2563*NFCA]}$			Decline at 300 m from natural habitat Without NFCAs → 72% fewer (i.e. 0·1 bees)			Decline at 300 m from natural habitat With NFCAs → 163% more (i.e. 0·3 bees)
Flying visitor species richness									
Model 1 (best model)	0·0003	0·0022	–	0·0056	–	64·9	77·3		
Model 2	0·0011	0·0085	–	–	–	70·6	80·9	5·7	3·6
Best model equation						Decline at 300 m from natural habitat Without NFCAs			Decline at 300 m from natural habitat With NFCAs
With pesticides			$Y = e^{0.9490-0.0021 \times DN\,[+0.5627*NFCA]}$			→ 47% fewer (i.e. 2·0 species)			7% fewer (i.e. 0·2 species)
No pesticides			$Y = e^{1.4613-0.0021 \times DN\,[+0.5627*NFCA]}$			→ 40% fewer species in orchards with pesticide			

AIC, akaike information criterion; BIC, Bayesian information criterion; NFCA, native flower compensation area.
The two most parsimonious models are listed, and the equation of the best model (lowest AICc) is provided for each subset whenever we found a significant effect of explanatory variables. Mixed model analyses are based on 62 surveys carried out in organic (nine far from NFCAs; five near NFCAs) and conventional orchards (12 far from NFCAs, six near NFCAs, see details in Table S2, Supporting information). *P*-values were obtained from a likelihood ratio test in which deviances with and without that term in the model were compared (n.s., $P > 0.05$). In the equations, NFCA is either 1 (present) or 0 (absent).

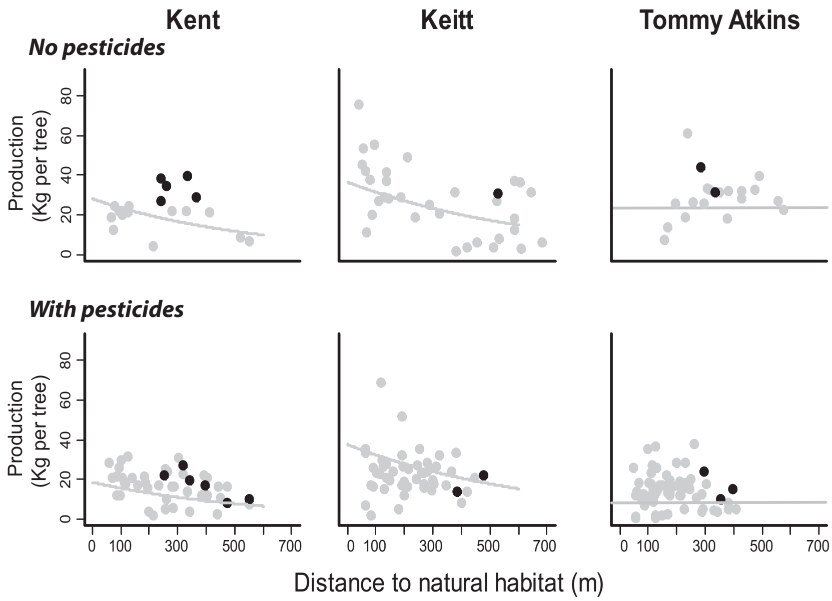

Fig. 3. Effect of distance to natural habitat, pesticide application and native flower compensation areas (NFCAs) on 2009 mango final production (kg of commercially suitable fruit per tree). Regression lines representing estimated production for orchards far from NFCAs are presented whenever the effect of distance from natural habitat was significant. For Tommy Atkins, where distance had no significant effect, the grey line represents the estimated mean production per orchard. Orchards near to NFCAs (black circles), had significantly higher production than orchards far NFCAs (grey circles, see Table 2 for statistical details).

300 m from natural habitat (see equations in Table 2). Production was significantly higher near to NFCAs, with an average an increase of 1·5 kg of commercially suitable mango per tree in all cultivars, production of these isolated orchards being closer to those of orchards near natural habitat (equations in Table 2, see black circles in Fig. 3). Production of Tommy Atkins (which did not vary significantly with isolation from natural habitat) increased by 55% close to NFCAs. In 2008, prior to creation of the NFCAs, production of orchards near the location of NFCAs was not significantly different to other orchards (see Table 2). Moreover, pesticide use had a negative effect on 2009 production for Kent and Tommy Atkins, although this effect was not found for Keitt.

With regard to ecosystem disservices, after 6 months, 30 insects had emerged from the seeds of *A. greatheadii*, (10 *Phortica* sp., Diptera: Drosophilidae; and 20 *Eurytoma* sp.1, Hymenoptera: Eurytomidae). No insects emerged from the 120 fruits collected from *B. obtusa*. None of the species reared in the preliminary surveys (Table S1, Supporting information) or within NFCAs are known pests of mango (J. T. Smit, pers. comm.).

EVALUATION OF COSTS AND GAINS RELATED TO NFCAS

Native flower compensation areas were created in nonproductive margins, so did not replace mango trees. Given that these plants occur naturally in the study region and mango fields are irrigated, no maintenance was required. As each NFCA influences an orchard area of at least 4 ha, the implementation of NFCAs in this study cost *c.* 56·3 USD per ha (including labour and costs of buying fully developed adult plants, see details in Table S5, Supporting information).

Our results estimated an average increase in production of 1·5 kg per tree (see Table 2). Average current price of a kilogram of mango across a spread of outlets, after deducting all marketing and packaging costs, is: Kent – 0·305 USD; Keitt – 0·315 USD; Tommy Atkins – 0·333 USD (J. du Preez, pers. comm.). As tree density was *c.* 747 trees per ha (information provided by farmers), implementation of NFCAs should lead to an average gain of 342–373 USD per ha. Because production cost is mainly determined per hectare and is not influenced by volume of crop to be harvested, all increase in volume will have a positive impact on the economics of the crop (J. du Preez pers. comm.). Therefore, after excluding costs of implementation of NFCAs (using fully developed plants), profit would be 285–317 USD per ha.

Discussion

Ongoing biodiversity decline and increasing demand for pollinator-dependent products in our diets make it a critical challenge to develop environmentally friendly agricultural practices to increase production. The costs of introducing patches of native plants into cropland might discourage farmers from introducing such measures (see Ghazoul 2007), but we found that small patches of native flora, planted in nonproductive margins of large mango orchards, enhanced abundance and diversity of mango

Table 2. Effect of distance to natural areas (DN), pesticide use (P) and NFCAs on 2008 (no NFCAs) and 2009 (with NFCAs) production (kg per tree) of all cultivars (C)

Response variable (Y)	DN *P*-value	P *P*-value	C *P*-value	NFCA *P*-value	DN*C *P*-value	P*C *P*-value	DN*P *P*-value	AICc	BIC	ΔAICc	ΔBIC
Production 2008											
Model 1 (best model)	<0·0001	0·0048	ns (0·20)	–	<0·0001	<0·0001	–	488·9	533·3		
Model 2	<0·0001	0·0048	ns (0·67)	ns (0·32)	<0·0001	<0·0001		490·1	537·8	1·2	4·5
Production 2009											
Model 1 (best model)	<0·0001	ns (0·66)	<0·0001	<0·0001	<0·0001	<0·0001	–	369·5	417·2		
Model 2	<0·0001	ns (0·66)	<0·0001	<0·0001	<0·0001	<0·0001	ns (0·07)	371·4	422·5	2·2	5·3
Best model equations for Production 2009							Production drop at 300 m from natural habitat				
No pesticide						No NFCA		With NFCA (1·5 kg increase)			
Kent		$Y = e^{3\cdot3370-0\cdot0017 \times DN\ [+0\cdot4175 \times NFCA]}-1$				→ 41% less		9% less			
Keitt		$Y = e^{3\cdot5986-0\cdot0015 \times DN\ [+0\cdot4175 \times NFCA]}-1$				→ 37% less		3·2% less			
Tommy Atkins		$Y = e^{2\cdot8969\ [+0\cdot4175 * NFCA]}-1$				→ no significant effect of distance but 55% more with NFCA					
With pesticides											
Kent		$Y = e^{2\cdot9191-0\cdot0017 \times DN\ [+0\cdot4175 \times NFCA]}-1$				→ 35% less production with pesticide use					
Keitt		$Y = e^{3\cdot1807-0\cdot0015 \times DN\ [+0\cdot4175 \times NFCA]}-1$				→ no significant effect of pesticide use					
Tommy Atkins		$Y = e^{2\cdot4790\ [+0\cdot4175 \times NFCA]}-1$				→ 36% less production with pesticide use					

AIC, akaike information criterion; BIC, Bayesian information criterion; NFCA, native flower compensation area.
The two most parsimonious models are listed, and the equation of the best model (lowest AICc) is provided for each subset. Analyses are based on 243 orchards, with farm (four groups) as random variable. *P*-values were obtained from a likelihood ratio test in which deviances with and without that term in the model were compared (n.s., $P > 0\cdot05$). In the equations, NFCA is either 1 (presence) or 0 (absence), its present leading to an average increase 1·5 kg of commercially suitable mango per tree

flower visitors, ameliorating the negative effects of isolation from natural habitat. These increases were associated with significantly higher mango production yields in all three major cultivars.

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO FLOWER VISITOR COMMUNITIES

Isolation from natural habitat had a negative impact on mango flower visitor diversity and abundance, consistent with earlier findings (Carvalheiro *et al.* 2010). Pesticide use negatively affected flower visitor abundance and diversity, contrary to findings in 2008 (Carvalheiro *et al.* 2010). Here, we detected more flying flower visitors (50 species in 2009; 26 species in 2008), and all orchards had managed honeybees present, unlike in 2008. These factors may have contributed to lower variability in our results for flower visitor numbers than the 2008 study, enabling detection of significant trends. Nevertheless, absence of pesticides did not offset effects of distance to native vegetation, which was significant in both organic and conventional farms. Such an offset might be expected in homogeneous landscapes with little or no natural habitat, where the only remaining flower visitors are able to nest within farmland, but not in richer landscapes (as in this study), where the diverse flower visitor community probably depends on various foraging, nesting and overwintering resources (see Rundlöf & Smith 2006; Holzschuh *et al.* 2007).

The presence of NFCAs facilitated crop visitation. Although the patches of planted floral resources were small (25 m^2), the plants used are highly attractive to flower visitors, eliciting an increase in orchard (orchard centre at 50–150 m) flower visitor abundance and diversity, ameliorating effects of distance to natural habitat. That, low-abundance flowering plants within agricultural lands can significantly increase flower visitors has been observed in crop fields with variable weed abundance (e.g. sunflower, Carvalheiro *et al.* 2011; watermelon and pepper, Winfree *et al.* 2008).

The beneficial effect of plant diversity might arise because a diversity of food resources is important for flower visitor health (Müller & Kuhlmann 2008; Alaux *et al.* 2010), and can also improve stability of pollinator assemblages (Ebeling *et al.* 2008), enabling adaptation to environmental changes. That, the two perennial species we used begin flowering before mango, and that NFCAs were not mowed during the study might also have helped, creating potential nesting areas for wild bees (see Williams *et al.* 2010), although in conventional fields, these areas will likely be adversely affected by insecticide applications, compromising continuity. While it is difficult to predict if two co-flowering species will compete with or facilitate each other for flower visitors, some studies suggest that facilitation is more likely between plants with unequal flower abundance (Ghazoul 2006) or that attractive species may facilitate less attractive species (Molina-Montenegro, Badano & Cavieres 2008). Larger NFCAs with more plant diversity could have achieved a larger effect than we found, and using two other species might have produced different results. Further studies are necessary to determine the optimum size, plant composition and spatial configuration of NFCAs for mango production.

Although we could not distinguish managed from wild honeybees, increased honeybee abundance on mangos near NFCAs suggests that provision of alternative floral resources by NFCAs encouraged foraging by managed honeybees within the orchards (hives present in all mango orchards, see Materials and methods). Nevertheless, diversity and abundance of flower visitors near NFCAs were still lower than in orchards near natural habitat (see Figs 1 and 2), where the pool of pollinators is larger. Therefore, ongoing habitat destruction in the landscape overall could negate this positive effect of planted patches.

EFFECT OF SMALL PATCHES OF PERENNIAL NATIVE FLORA ON MANGO PRODUCTION

Both abundance and diversity of flower visitors are important to crop pollination efficiency (Kremen, Williams & Thorp 2002; Carvalheiro *et al.* 2010) and stability (Klein 2009; Winfree & Kremen 2009). Here, we found that although final production of several mango cultivars is negatively affected by isolation from natural habitat and pesticide use, these effects can be ameliorated (but not totally remedied) by the presence of floral resources within farmland.

The effect of distance to natural habitat and the presence of NFCAs on crop production of Kent and Keitt, but not on early fruit set, might be explained by the type of pollination taking place. Ants have been found to be important in pollination of mango elsewhere (Free & Williams 1976; Anderson *et al.* 1982) and in this study area, contributing to *c.* 50% of the early fruit set, but are not influenced by distance to natural habitat (Carvalheiro *et al.* 2010; this study). Ants, however, are not very mobile and are more likely to contribute to self- than cross-pollination, potentially leading to fruit abortion (e.g. Papadakis, Protopapadak & Therio 2009; Sousa, Pigozzo & Viana 2010).

Pollen supplementation experiments comparing cross and self-pollination would help clarify the importance of cross-pollination. Nevertheless, these results are consistent with our previous mango pollination study (Carvalheiro *et al.* 2010), where models assuming that early fruit set due to self, ant and flying visitor pollination were equally likely to contribute to final production underestimated the negative effect of isolation from natural habitat on production. This suggests that early fruit set measurements (1–2 months before harvesting, see methods in Carvalheiro *et al.* 2010) overestimate the contribution of ants and/or self-pollination to final production. Moreover, honeybees were markedly influenced by the presence of NFCAs, suggesting that although bees tend not to be attracted to mango (Carvalheiro *et al.* 2010), if enticed to forage within mango fields they can contribute to mango pollination. Exclusion experiments on each cultivar would also show whether a higher self-pollination ability of Tommy Atkins (see Sousa, Pigozzo & Viana 2010) explains the lack of effect of declining flower visitors with isolation from natural habitat on final production of this cultivar.

Pesticide use was associated with declines in fruit production of two cultivars. However, mangoes produced on our study farms are used for both fresh and processed products. Production data obtained from farmers includes fruits damaged by pests (used for processed products, farmers' communication), removing the importance of pest damage on final production figures. As farmers sell their product per kg and not per mango, weight is a good indicator of economic profit. However, 1 kg of fresh fruit that will be processed is worth less than 1 kg of fresh fruit that will be sold as such. Further analysis of processed and fresh fruit production would yield a more detailed evaluation of the effect of pests and pesticide use on production. The lack of a negative effect of pesticide use for Keitt cultivar might be attributable to the low number of available orchards (see Table S2, Supporting information), and its relatively low attractiveness to flower visitors (see Fig. 1).

While a detailed economic evaluation would have to take into account fruit quality, our results indicate that no negative effects on production are expected from widespread use of NFCAs (using *A. greatheadii* and *B. obtusa*) in all mango orchards. Profitability largely depends on their success in attracting pollinators to mango fields, considerable increased profit being obtained even with small NFCAs. Moreover, while in our study, we used adult plant specimens purchased from nurseries, costs could have been reduced by growing plants from seeds.

IMPLICATIONS FOR SUSTAINABLE FARMING

The use of patches of alternative floral resources to promote biodiversity within farmland, stimulated via government subsidies in some countries, has been found to have variable success in restoring arthropod communities (Kleijn & Sutherland 2003). Here, we found that for a perennial pollinator-dependent crop, creation of NFCAs can be profitable, improving production within existing plantation areas while contributing to conservation of biodiversity within the region indirectly (reducing the need for agricultural expansion) and arguably directly (by increasing habitat and resources for insect species within farms, particularly if the set of species used guarantees flowering throughout the year). Annual crops might also benefit from enhanced floral diversity (e.g. Carvalheiro *et al.* 2011). However, for perennial tree crops such as mango, negative effects of nonparasitic flowering low growth form perennials, such as our experimental plants, are less likely.

The benefits of NFCAs might increase with time, as more invertebrates use the foraging and nesting resources provided by these patches of less-disturbed habitat. Future studies with NFCAs of varying size, composition and distance to natural habitat, with measurements of productivity at different distances from NFCAs, are needed to clarify the extent of NFCA economic benefits. Moreover, while NFCAs are likely to be favourable to common and widespread flower visitor species (e.g. Kleijn *et al.* 2006), rarer species, which can enhance resilience of agricultural landscapes to future environmental changes, might not benefit.

FINAL RECOMMENDATIONS

Farmers often remove weeds from agricultural fields through fear of competition for soil resources and flower visitors. Our study adds to a growing body of evidence (e.g. Winfree *et al.* 2008; Carvalheiro *et al.* 2011) that the presence of flower diversity before and during crop flowering facilitates, rather than reduces, pollination of the hyper-abundant crop flower resource. These increases ameliorate (but do not totally compensate for) negative effects of isolation from natural habitat on productivity of pollinator-dependent crops. While costs involved in planting NFCAs may discourage farmers from implementing such measures (Ghazoul 2007), here we found that even small NFCAs can increase flower visitor abundance and diversity, and overall economic profit can justify their creation. Combined with preservation of remaining fragments of natural habitat and reduced pesticide use, NFCAs could help maximize yield of pollinator-dependent crops, minimizing the need for agricultural expansion, and contributing to sustainable farming.

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Supporting Information

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

Fig. S1. Field site and experimental layout.

Fig. S2. Flower abundance of plants in NFCAs.

Fig. S3. Variation of early fruit set with isolation from natural habitat.

Fig. S4. Variation of mango ant visitors (abundance and diversity) with isolation from natural habitat and pesticide use.

Table S1. Fruit herbivores and parasitoids reared from fruits of Aloe *greatheadii* and *Barleria sp*. plants present in natural areas surrounding the studied farms.

Table S2. Study orchard details.

Table S3. Effect of spatial autocorrelation on mango flower visitation and production.

Table S4. Flower visitor list for all studied cultivars of mango and in NFCAs.

Table S5. Evaluation of costs of NFCAs.

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