

Local and landscape effects on bee functional guilds in pigeon pea crops in Kenya

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Received: 22 December 2014 / Accepted: 11 July 2015 / Published online: 16 July 2015
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Abstract Pollinators face many challenges within agricultural systems due to landscape changes and intensification which can affect resource availability that can impact pollination services. This paper examines pigeon pea pollination and considers how landscape context and agricultural intensification in terms of pesticide use affects the abundance of bees characterized by species guilds on crops. The study was conducted on six paired farms across a gradient of habitat complexity based on the distance of each farm from adjacent semi-natural vegetation in

Kibwezi Sub-county, Kenya. The study found that farms which do not use insecticides in farm management, but are in close proximity to natural habitat have greater bee guild abundance, but at further distances, overall abundance is reduced with or without insecticide use. At 1 km landscape radius, the complexity of habitats but not patch size had a positive impact on the abundance of cavity nesting bees and mason bees, which can be attributed to the interspersed of the small-holder farms with semi-natural habitats across the landscapes producing mosaics of heterogeneous habitats. The study revealed the strongest relationships between fruit set and bee abundance to be with the carpenter bee, social bee and solitary bee guilds, which are among the most abundant bees visiting pigeon pea flowers in this system. Our findings provide the foundation for conservation efforts by identifying which bee guilds pollinated pigeon peas. From this study, we suggest managing the floral and nesting resources that would best support the most abundant crop pollinators, and also reducing insecticide application to the crop.

Electronic supplementary material The online version of this article (doi:10.1007/s10841-015-9788-z) contains supplementary material, which is available to authorized users.

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Keywords Functional group · Landscape effects · Pesticide · Semi-native · Species guild · Tropical agroecosystems

Introduction

Bees provide the critical ecosystem service of pollination (Garibaldi et al. 2013), and as free-foraging organisms, they face many challenges within agricultural systems due to intensification (Kremen et al. 2002; Tschamtkke et al. 2005). Broadly, agricultural intensification includes increased inputs of agro-chemicals, decreased crop diversity, and reduction of adjacent natural and semi-natural

habitats (Tscharnke et al. 2005; Garibaldi et al. 2013; Deguines et al. 2014). These changes cause alterations in the spatial–temporal distribution of resources for insect pollinators, and reduce resource availability which can contribute to overall pollinator decline (Kremen et al. 2002; Tscharnke et al. 2005; Winfree et al. 2007; Ricketts et al. 2008; Rundlof et al. 2008; Potts et al. 2010; Cameron et al. 2011).

Challenges for pollinators arise at both the local farm management level as well as the larger landscape level, both of which can affect pollination services. At the local farm-level increased inputs, such as insecticide usage, can negatively impact pollinator populations through direct and indirect exposure (Brittain et al. 2010a, b), which can also reduce pollination efficiency (Sabatier et al. 2013; Feltham et al. 2014).

At the larger landscape-level, challenges due to intensification include increased habitat fragmentation and simplification of landscapes that result in habitat isolation and reduced abundance and diversity of floral and nesting resources (Garibaldi et al. 2011; Ferreira et al. 2013) that are unable to support diverse pollinator communities (Tscharnke et al. 2005; Andersson et al. 2013). Proximity of crop fields to semi-natural vegetation is important in enhancing pollinator diversity and the level of pollination to crops (Karanja et al. 2010; Blitzer et al. 2012; Klein et al. 2012); However, proximity to semi-natural vegetation may vary with the landscape context (Steffan-Dewenter et al. 2002; Ricketts et al. 2008; Jha and Kremen 2013). The reduction of supportive natural habitat also reduces pollinator abundance in adjacent field crops, which negatively impacts pollination services within agricultural systems (Steffan-Dewenter et al. 2002; Ricketts et al. 2008). Indeed, several studies have established close correlations between increasing agricultural intensification and declining abundance and diversity of insect pollinator species (Kremen et al. 2002; Hendrickx et al. 2007; Hagen and Kraemer 2010) and resulting decline in crop yield (Klein et al. 2003; Isaacs and Kirk 2010; Otieno et al. 2011).

Many pollinator-based landscape studies focus on the response of bee communities to species richness, abundance and pollination efficiency (e.g. recently Ricketts and Lonsdorf 2013; Williams and Winfree 2013; Andersson et al. 2013; Bailey et al. 2014). The conclusions of these studies provide information that benefits land management efforts for specific agricultural systems. An example is the establishment of agri-environmental schemes (AES) throughout Europe, which aims to reduce biodiversity loss (Kleijn and Sutherland 2003). Additional management strategies include mitigating habitat fragmentation (Harrison and Bruna 1999), preserving natural habitat (Kremen et al. 2004), and providing additional foraging and nesting resources for free-foraging pollinators (Scheper et al. 2013).

Yet, whilst these studies are used to understand pollinator relationships to the environment, most are limited to North America and Europe; few studies consider African and Asian agricultural systems (Archer et al. 2014). These systems face similar agricultural intensification, but differ in pollinator communities and agricultural cycles. Thus conclusions from most pollinator studies cannot be readily transferred into other agricultural systems worldwide.

In this study we focused on the pollinators in the economically important pigeon pea [*Cajanus cajan* (L.) Millsp.: Leguminosae] agricultural system in Kenya. Pigeon pea is a dominantly grown crop in the dry Lower Eastern regions of Kenya covering approximately 150,000 ha and mainly used for human dietary protein provision and fodder for animals (Otieno et al. 2011). We considered the effects of agricultural intensification on species richness, abundance and pollination efficiency, and we further considered bee abundance in relation to species guilds. Here, a guild is defined as a group of species that utilize related resources in similar ways (Simberloff and Dayan 1991). By grouping bees into guilds we can identify common patterns of response to agricultural intensification pressures within a habitat and transfer them into other habitats with completely different species communities that share similar guilds. Conclusions from this study using species guild abundances will benefit this specific crop in Africa and other tropical regions. Moreover, the results can also be used to increase the generality of findings beyond the specific habitat within which they were undertaken (Williams et al. 2010; Blaum et al. 2011).

For this study our aim was to examine the pigeon pea cropping system by evaluating how agricultural intensification affects the pollinator community as characterized by species guilds. Specifically, we asked the following questions: (1) How do local and landscape factors impact on the abundance of pollinator guilds? (2) What are the patterns of bee abundance when farms are farther from semi-natural vegetation and either sprayed with insecticides or not compared to those closer to semi-natural habitats? (3) Is there a difference in fruit set when pollinators are excluded from flowers or not?

Agricultural intensification was characterized by: landscape complexity, which captures resource diversity; proximity of a field to natural habitat, which captures resource accessibility; and management practices, such as insecticide application, which may negatively impact pollinators. We characterized bee guilds by key traits such as nesting, sociality, and diet breadth, which are related to habitat requirements. Pollination efficiency was measured by comparing restricted self-pollination with open pollination. This study highlights conclusions relevant to Kenyan agriculture, but also conclusions that are transferable among ecosystems worldwide.

Methods

Site selection

We conducted the study in Kibwezi Sub-county, Makueni County, Kenya (2°15'S and 37°45'E) at 723–1015 m above sea level, about 150 km South East of Nairobi from April to June 2009. The climate is broadly characterized by annual temperatures reaching 30 °C and annual rainfall of 644 mm (Mbuvi 2009). The landscape is generally comprised of rain-fed agricultural fields that rely completely on natural precipitation, and non-cropped patches of semi-natural vegetation adjacent to crop fields that are comprised predominantly of native plants.

We selected six pairs of pigeon pea crop fields along a gradient of landscape heterogeneity totaling 12 sites. Each pair had a simple and a complex site in a similar area determined using a land use/land cover (LULC) map with a 1 km radius buffer surrounding each field. Landscape heterogeneity ranged from simple landscapes characterized by a high percentage of arable land (>50 % cropped fields) within the 1 km buffer at each site to complex landscapes (<50 % cropped fields) within the same spatial landscape radius. We maintained a minimum distance of 2 km between the site pairs as determined using LULC maps in ArcGIS 9.3 so that pollinator communities did not overlap. We used the LULC map derived from a Landsat 7 Enhanced Thematic Mapper image (2003) ground truthed in April 2009 to check the accuracy and consistency of different land cover types.

Agricultural intensification

Proximity to natural habitat

To assess the effects of this factor on species guilds, we categorized each site of each pair based on its proximity to semi-natural habitat which is important for resource accessibility to pollinators (Rathcke and Jules 1993). Of the 12 study sites assigned into six pairs, we had a total of six far sites and six near sites. “Far” sites were typically located in a simple landscape more than 200 m from the nearest non-cropped patch and were dominated by a mix of cropland and human habitation; “near” sites were located in a complex landscape <200 m from non-cropped patches (Otieno et al. 2011; Sabatier et al. 2013; Feltham et al. 2014). We used “far” and “near” as categorical explanatory variables for further analysis.

Insecticide usage

To assess the field management used on each site, we conducted face-to-face interviews with farmers and

concluded that insecticide usage was a key farm management practice. This emerged as the most consistent practice either used or not used by farmers. The active ingredients in the insecticides applied across the study sites were: Thiamethoxam; Dimethoate; Alpha-Cyphpermethrin; Beta-Cyfluthrin; Lambda Cyhalothrin; Azoxystrobin and Methomyl (see Appendix S1 for common names and target pests). We therefore used the number of applications of insecticide per crop season as an indication of local management intensity for the pigeon pea crop.

Landscape complexity

We derived metrics to measure landscape context to quantify agricultural intensity using the Patch Analyst extension in ArcGIS 9.3 (Elkie et al. 1999; Ferreira et al. 2013) based on the 1:500,000 LULC maps described above. We selected non-collinear landscape metrics following a collinearity test (Table 1). The selected metrics have been shown to have a significant ecological influence on pollinators (Barbaro et al. 2005; Tschardt et al. 2005; Steffan-Dewenter et al. 2005; Andersson et al. 2013) (Table 1). These were: (1) mean shape index, which is a measure of patch complexity taking into account the perimeter and area of each patch type within the 1 km landscape radius (McGarigal and Marks 1994; Elkie et al. 1999; Steffan-Dewenter et al. 2002; Ricketts et al. 2008), used to measure the effects of landscape structure on pollinators (Coulson et al. 2005; Krupke et al. 2012); (2) mean patch size, which is the mean number of patches of different sizes at the site and (3) edge density of non-cropped patches, which is the amount of habitat patch edge within a landscape area (i.e. 1 km radius here). Edge density measures landscape configuration, and is important in making comparisons between landscapes of variable complexities and sizes and how that affects resource availability to animals. Collectively, these metrics provide a quantitative description of landscape complexity.

Pigeon pea pollinators

Bee abundance and species richness

Bee abundance was measured by observing bee visitation to flowers. Bees were observed along five 100 m transects at each pigeon pea crop field; transects were placed north to south, each separated by a minimum of 10 m at each site. Bee visitations within 2 m of the transect were recorded as we walked each transect for 10 min, twice a day (between 0900 and 1600 h). A total of 49 days were spent to sample all the 12 sites between 20th April and 20th June 2009. Bee species richness was quantified by collecting bees and identifying them to species or to morphospecies, for those

Table 1 Correlation matrix of landscape metrics generated by Patch Analyst within ArcGIS 9.3 at 1 km spatial radius

	MPS	TE	ED	MSI	MPFD	TCA	LPI
Mean patch size	1.00						
Total edge	0.40	1.00					
Edge density	0.40	1.00	1.00				
Mean shape index	0.21	0.83	0.83	1.00			
Mean patch fractal dimension	0.33	0.80	0.80	0.97	1.00		
Total core area	0.91	0.52	0.52	0.15	0.27	1.00	
Largest patch index	0.92	0.55	0.55	0.21	0.33	0.99	1.00

MPS mean patch size, *TE* total edge, *MSI* mean shape index, *MPFD* mean patch fractal dimension, *TCA* total core area, *LPI* largest patch index of each habitat patch

which available keys could not identify them to species, by aid of reference collection and bee experts at the National Museums of Kenya, York University and University of Pretoria.

Bee abundance by guild

Bee guilds were categorized based on a compilation of ecological and life histories from the existing literature (Michener 2000; Blaum et al. 2011; Garibaldi et al. 2013). We then identified and assigned three of the most ecologically relevant and widely used traits (Kremen et al. 2002; Tscharrntke et al. 2005; Moretti et al. 2009; Woodcock et al. 2009; de Bello et al. 2010; Bommarco et al. 2010; Williams et al. 2010) to each bee species/morphospecies for further analysis. We considered the following traits: sociality, diet breadth, and nesting specialization to delineate bee guilds. Sociality traits were categorized as: social bees, semi-social bees, solitary bees. Diet breadth traits were categorized as: oligolectic bees, and polylectic bees. Nesting traits were categorized as: carpenter bees, soil cavity nesting bees, mason bees, above ground cavity nesting bees (e.g. honey bees), and no-nest bees. (See Table 2 for detailed description and species groupings and Appendix S2 for species trait information). These guilds were created to include the most relevant natural history traits that are related to bee resource requirements and are also commonly studied in the functional ecology of insects.

Pollination services

Crop response was measured by quantifying pollination services. This was done by determining the proportion of fruit set attributable to insect pollinators using paired comparisons of pigeon pea crop either open or closed to insect pollinators (Tscharrntke et al. 2005; Ricketts et al. 2008; Garibaldi et al. 2013; Deguines et al. 2014). We selected three plants in each transect within the crop at 5, 50 and 95 m totaling 180 plants across all sites (3 plants per transects × 5 transects × 12 sites = 180). Each plant

we selected had at least two branches (50 cm long each) with unopened flower buds. We covered one of these branches with a fine cloth netting (Tulle bag) to stop insect pollen vectors. We left open the other branch as a control (open pollinated). We counted the number of pods (fruit) set on both the experimental and control branches per plant at the end of the experiment and quantified the amount of pollination due to insects following the formula from Ricketts et al. 2008.

$$\text{Insect Pollination} = \text{Open pollination} [\text{control}] - \text{Self-pollination} [\text{Tulle bags}].$$

In the analysis, fruit set attributable to bees was quantified as the percentage of the difference between open and closed pollination.

Data analysis

We summed bee data and fruit set from each field for the entire sampling period and analyzed these using linear mixed effects models (lmer, lme4 package) in R for Windows version 2.15.2 (R Core Team 2013) (e.g. Kremen et al. 2002; Steffan-Dewenter 2003; Neumann and Carreck 2010; vanEngelsdorp et al. 2010; Otieno et al. 2011) to relate proximity to natural habitat, insecticide use, landscape complexity and pollination services with bee abundance.

Each model was fitted with five fixed effect explanatory factors and site as a random effect. The fixed explanatory factors were: (a) proximity to natural habitat and (b) the number of insecticide applications (c) mean shape index, (d) mean patch size and (e) edge density. A mixed effect model was constructed for each response variable, which were total bee abundance, overall bee species richness, and each bee guild as characterized by sociality, diet breadth and nesting trait (listed previously, Table 2). The data had higher variance than the means, so each model was fitted with Poisson errors, which are typically suited for count data with this distribution (Harrison and Bruna 1999; Bates 2010; Crawley 2012; Kéry and Schaub 2012). We specified the best model structure using a random intercept and slope

Table 2 Bee functional trait description and functional groups under each trait used for analysis

Trait groups	Categories	Definition
Social status	Solitary	Single adult constructs and provisions nest
	Social	Colonial life form, single reproductive adult with multiple worker, non-reproductive adults
	Semi-social	Shows primitive social life history. Multiple adults functioning in colony, division of labor among adults
Feeding specialization	Oligolectic	Forages on limited resources and requires specific components from the habitat
	Polylectic	General forager utilizing a broad range of floral resources
Nest specialization	Carpenter	Excavates (drills nests in wood)
	Miners	Excavate nests in the ground
	Renters	Nests in existing aerial tunnels and cavities (e.g. trees, fallen logs, stems)
	Soil cavity nesters	Nests in existing tunnels and cavities in the soil e.g. old termite mounds
	Mason	Builds nests with mud
	No nest	Cleptoparasites or parasitic, occupy other bee nests

Trait groups were determined based on published literature. Each trait category was calculated from pooled bee abundance per site. Different functional groups of traits per trait group were analysed to determine the response of each to landscape structure and local site conditions/management

models and compared the fit of individual models using the Akaike information criterion (AIC) (Kleijn and Sutherland 2003; Bates 2010; Crawley 2012). In this process, we compared models with and without one explanatory variable to obtain a minimum adequate model with the lowest AIC number.

Pollination service was also measured with a similar linear mixed effects model structure with fruit set as the response variable. Pollinator abundance and species richness were included as fixed terms in addition to the explanatory and categorical variables in the model. The interactions between proximity to natural habitat, the number of insecticide applications and each of the landscape effect terms were non-significant and not included in the model.

To determine the patterns of bee abundance when farms were farther from semi-natural vegetation and either sprayed insecticides or not compared to those closer to semi-natural habitats, we averaged data across sites and performed a generalized linear mixed-effects model (glmer, lme4 package) with Poisson error distribution (Bates 2010; Chateil and Porcher 2014). Here, we had two categorical fixed factors: local proximity to natural habitat (either near or far) and insecticide use (either yes or no). Site was included as a random effect. We tested for the effect of interactions between local proximity to natural habitat and insecticide use on the abundance of each of the bee traits (Table 2) used in the previous analysis as response variables.

Paired sample *t* tests were used to assess the difference between fruit set when pollinators were excluded from

flowers or not. Simple regression models were run to test for linear relationships between the abundance of bees of different traits and fruit set.

Results

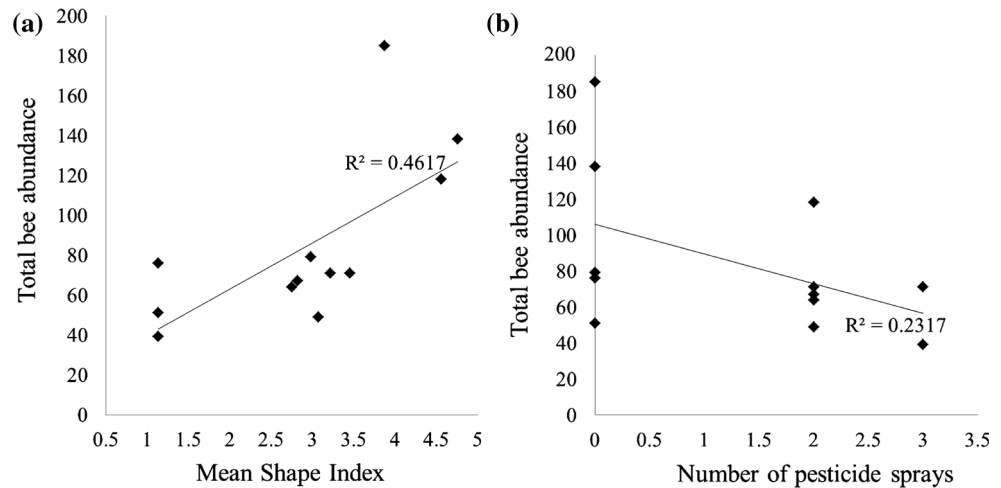
Pollinators in the pigeon pea system

We recorded a total of 1008 bee visitors from 31 genera. The most abundant bees were *Megachile* spp. (Megachilidae: Hymenoptera) (28.57 %), *Apis mellifera* (Apidae: Hymenoptera) (19.94 %), *Ceratina* spp. (18.35 %) and *Xylocopa* spp. (6.85 %). *Megachile* spp. are all solitary (eight species) and mostly soil cavity nesting, with one mason species. *A. mellifera* are social and above-ground cavity nesters. *Ceratina* spp. and *Xylocopa* spp. are both semi-social and categorized as carpenter bees. All of the most abundant species are polylectic bees.

The impacts of local and landscape factors on overall bee abundance and species richness

At the farm level, the number of insecticide applications had a significant negative impact only on the total bee abundance ($z = -6.537$, $p < 0.001$; Fig. 1b), but not species richness ($z = -1.658$ and $p > 0.05$). Out of all the landscape complexity metrics used to characterize agricultural intensification, only mean shape index (i.e. patch complexity) had a significant positive effect on total bee abundance ($z = 4.76$, $p < 0.001$; Fig. 1a), whereas mean

Fig. 1 Relationship between **a** landscape complexity (measured by mean shape index metric) and total bee abundance and **b** number of insecticide spray and total bee abundance. Values at “0” on the x-axis (e.g. 1a) indicate fields with no insecticide application



patch size and edge density did not have a significant effect on species richness or bee abundance.

The impacts of local and landscape factors on of bee guilds

Proximity of sites to natural habitat patches at the local scale had a significant effect on the abundance of mason, miner and polylectic bees. We found significantly higher numbers of mason bees in fields farther away from semi-natural habitat patches (Table 3). We found the opposite effect of the proximity of sites to semi-natural habitats on mining bees and polylectic bees (Table 3).

The number of insecticide applications on pigeon pea crops had significant negative effects on the abundance of carpenter bees, bees nesting in soil cavities and mining bees (Table 3). Similarly, we detected significant negative effects of the number of insecticide applications on social, solitary, and semi-social bees (Table 3). However, only polylectic bees of the two lecty traits examined were negatively affected by the number of insecticide applications (Table 3).

Habitat complexity had various effects on bee diversity when bees were considered by guild. At the 1 km spatial scale, mean shape index had significant positive effects on the abundance of cavity nesting bees and mason bees (Table 3). Conversely, for the sociality traits only solitary bee and polylectic bee abundance was significantly positively affected by mean shape index (Table 3). Mean patch size had significant positive effects on carpenter bee and mason bee abundance (Table 3). We found a similar effect with edge density on carpenter bees and mason bees (Table 3).

With regards to the patterns of bee abundance when farms were farther from semi-natural vegetation and either sprayed insecticides or not compared to those closer to semi-natural habitats, proximity to semi-natural habitats

was the key factor affecting all functional guilds except cleptoparasites and oligolectic bees (Table 4). Carpenter bees were significantly more abundant on farms that were near semi-natural habitats. However, there was no difference in the abundance of these bees on sites farther from semi-natural vegetation whether they sprayed insecticides or did not. Similar results were obtained for soil cavity nesters, miners and above ground cavity nesters (Table 4). There was no effect on mason bees although mason bees were more abundant on farms farther from semi-natural vegetation that did not spray insecticides. Bees with no nests could not be modeled using interaction terms of insecticide use and proximity to semi-natural habitat most likely due to their very low abundance and hence low statistical power.

Polylectic bees were significantly more abundant on farms closer to semi-natural vegetation that did not spray insecticides (Table 4). The abundance of these bees on sites farther from semi-natural habitat (whether they sprayed insecticides or not) did not differ. Similar to bees without nests, oligolectic bees could not be modeled given the reason above.

The abundance of semi-social and social bees was affected by a significant interaction between proximity of sites to semi-natural habitat and insecticide use with far sites that did not spray having significantly more of these bee guilds than near sites that sprayed (Table 4). For solitary bees, although their abundance was significantly more on sites closer to semi-natural habitats, there was no difference in their abundance on sites farther from semi-natural habitats regardless of insecticide use.

Pollination services

Overall, there was a significant decline in the pigeon pea fruit set when pollinators were excluded from the system ($t = -7.88$, $p < 0.001$), with mean fruit set being almost

Table 3 Z-values of the outputs of linear mixed effects models showing results of the impact of landscape complexity (mean shape index), patch size (mean patch size) and configuration (edge density); local proximity to semi natural habitats and management [number of insecticide application (number of sprays)] on the abundance of bees and functional traits

Response factors	Fixed effects from the minimum adequate model				
	Local factors		Landscape factors		
	Local proximity to semi natural habitats	No. insecticide application	Mean shape index	Mean patch size	Edge density
(a) Total bee abundance		-6.537***	4.76***		
(b) Total bee species richness		-1.658			
(c) Nesting					
Carpenter (N = 262)	-	-4.954***	-	3.26**	5.02***
Soil cavity (N = 300)	-	-4.262***	8.215***	-	-
Mason (N = 29)	2.441*	-	-2.313*	2.218*	2.319*
Miner (N = 172)	-4.557***	-3.803***	-	-	-
Renter (N = 235)	0.236	-1.462	0.024	0.859	0.71
No nest (N = 10)	0.483	0.62	-0.388	0.68	0.642
(d) Sociality					
Semi social bees (N = 266)	-	-5.082***	-	3.262**	5.214***
Social (N = 290)	-	-3.729***	-	3.222**	5.845***
Solitary (N = 452)	-	-4.247***	8.115***		
(e) Diet breadth					
Oligolectic (N = 17)	-0.286	1.449	0.667	-0.343	-0.728
Polylectic (N = 991)	-2.115*	-6.736***	4.635***	-	-

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

halved in the absence of insect pollinators (mean number of fruits per 50 cm branch with pollinators = 42.08 ± 3.76 ; without = 24.58 ± 2.86). Independent of this overall effect, none of the local management or landscape factors were identified as having a significant effect on the difference in fruit set between open and closed treatments. Total bee abundance significantly correlated with fruit set ($p = 0.022$). Using separate regressions for each trait with fruit set, we found a significant positive relationship between the abundance of carpenter bees and fruit set ($R^2 = 0.63$, $F_{1,10} = 17.11$, $p = 0.002$; Fig. 2a). We found a similar effect on fruit set with social bee abundance ($R^2 = 0.34$, $F_{1,10} = 5.06$, $p = 0.048$; Fig. 2b) and solitary bee abundance ($R^2 = 0.40$, $F_{1,10} = 6.76$, $p = 0.026$; Fig. 2c). None of the other traits measured correlated with fruit set ($p > 0.05$).

Discussion

The impacts of local and landscape factors on of bee abundance and guilds

Our study shows that farms which do not use insecticides but are in close proximity to natural habitat have greater

bee abundance, but at further distances, overall abundance is reduced with or without insecticide use. Natural habitats, for example forest edges, form important refugia for pollinators. Our results, although done on a different cropping system (pigeon pea), are comparable to Bailey et al. (2014) who found the edges of semi-natural vegetation to support a large number of ground nesting bees in oil seed rape fields. These results confirm that natural habitat edges surrounding crop fields play an important function in providing extra food, pollinator nesting sites and even breeding and oviposition sites (Roulston and Goodell 2011; Carvalheiro et al. 2010; Smith et al. 2013; Bailey et al. 2014; Nayak et al. 2015). Cavity nesting bees, above ground nesting bees, polylectic, semi-social, social and solitary bee foragers were significantly more abundant closer to the semi-natural habitat than they were farther into the field. These bee species, commonly live within natural or semi-natural vegetation. Cavity-nesting bees have been shown to respond negatively to intense agriculture, presumably in response to loss of nesting habitat availability (Sheffield et al. 2013).

The inability to model the interactive effects of proximity of crop fields to natural habitat and insecticide use on oligolectic bees and bees with no nests is most likely caused by the low abundance resulting into low statistical

Table 4 *t*-Values of linear mixed effects models showing bee guild trait responses to proximity of sites to semi-natural habitats and insecticide application

Bee guild	Bee trait	Fixed factor	Estimate	SE	z-Value	<i>p</i>
Nesting	Carpenter	Local—near	3.26	0.29	11.09	<0.001
		Local—far	−0.27	0.19	−1.40	0.16
		Insecticide use—no	0.47	0.31	1.51	0.13
		Insecticide use—yes	−0.33	0.27	−1.23	0.22
		Local: insecticide use	−0.47	0.27	−1.75	0.08
	Cavity soil	Local—near	3.51	0.43	8.25	<0.001
		Local—far	−0.63	0.30	−2.10	0.04
		Insecticide use—no	0.27	0.43	0.65	0.52
		Insecticide use—yes	−0.30	0.39	−0.77	0.44
		Local: insecticide use	−0.46	0.40	−1.15	0.25
	Mason	Local—near	0.69	0.82	0.85	0.40
		Local—far	0.69	0.65	1.07	0.28
		Insecticide use—no	−0.29	1.00	−0.29	0.77
		Insecticide use—yes	−0.69	0.65	−1.07	0.28
		Local: insecticide use	0.69	0.91	0.76	0.45
	Miner	Local—near	3.44	0.35	9.70	<0.001
		Local—far	−0.66	0.25	−2.65	0.01
		Insecticide use—no	−0.10	0.38	−0.28	0.78
		Insecticide use—yes	−0.78	0.33	−2.37	0.02
		Local: insecticide use	−0.32	0.36	−0.88	0.38
Above-ground cavity nester	Local—near	3.31	0.30	10.91	<0.001	
	Local—far	−0.42	0.19	−2.19	0.03	
	Insecticide use—no	0.20	0.33	0.62	0.53	
	Insecticide use—yes	−0.28	0.28	−0.97	0.33	
	Local: insecticide use	−0.53	0.30	−1.77	0.08	
No nest	∞	∞	∞	∞	∞	∞
	∞	∞	∞	∞	∞	∞
Diet breadth	Polylectic	Local—near	4.76	0.21	22.55	<0.001
		Local—far	−0.50	0.15	−3.32	<0.001
		Insecticide use—no	0.23	0.22	1.04	0.30
		Insecticide use—yes	−0.38	0.19	−1.96	0.05
		Local: insecticide use	−0.31	0.20	−1.55	0.12
Oligolectic	∞	∞	∞	∞	∞	∞
	∞	∞	∞	∞	∞	∞
Sociality	Semi-social	Local—near	3.12	0.30	0.31	<0.001
		Local—far	−0.23	0.19	−1.22	0.22
		Insecticide use—no	0.67	0.32	2.10	0.04
		Insecticide use—yes	−0.20	0.28	−0.73	0.46
		Local: insecticide use	−0.54	0.27	−2.03	0.04
	Social	Local—near	3.64	0.27	13.44	<0.001
		Local—far	−0.42	0.18	−2.29	0.02
		Insecticide use—no	0.29	0.29	0.99	0.32
		Insecticide use—yes	−0.51	0.25	−2.05	0.04
		Local: insecticide use	−0.87	0.28	−3.09	<0.001
	Solitary	Local—near	4.13	0.36	11.36	<0.001
		Local—far	−0.64	0.26	−2.40	0.02
		Insecticide use—no	−0.15	0.36	−0.42	0.68
		Insecticide use—yes	−0.45	0.33	−1.37	0.17
		Local: insecticide use	0.07	0.34	0.21	0.83

∞ denotes failure of model to converge due to low abundance

* *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001

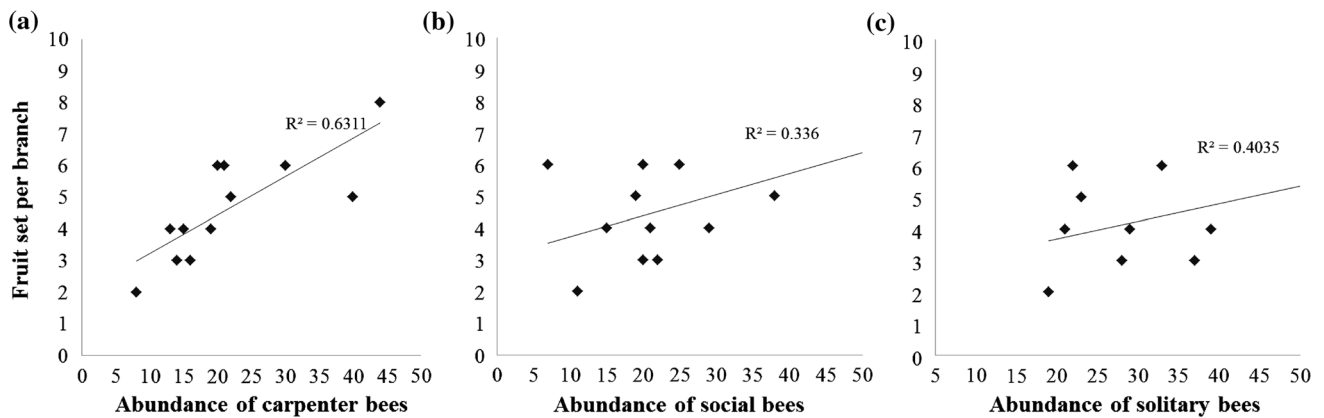


Fig. 2 Relationships with significant positive correlation between fruit per branch and **a** abundance of carpenter bees, **b** abundance of social bees and **c** abundance of solitary bees

power. The study findings for these bee guilds need to be treated with caution when dealing with large abundances as the response to the tested parameters may differ. It is recommended that more precise methods of sampling the less abundant groups be adopted to determine how they respond to proximity to semi-natural vegetation and insecticide application.

Insecticides had a negative effect on bee abundance. When the impact of insecticides was assessed by guild, there was a significant negative effect on the abundance of most bee guilds, which included: carpenter bees, soil nesting bees, miner bees, polylectic bees, and bees of all sociality types. Pollinators of pigeon pea crops could be affected by insecticide use due to traits captured by guild characteristics. Nesting sites may make some bees more vulnerable to lethal or sublethal effects (Brittain et al. 2010a, b; Brittain and Potts 2011; Krupke et al. 2012). Furthermore, diet breadth and exposure to insecticides and insecticide drift may impact bees (especially oligolectic) bees at a higher rate due to limited and concentrated food sources (Brittain and Potts 2011). However, polylectic bees in this study system do not have many wild nectar sources (M.O. personal observation) other than from other crops planted as intercrops, a common practice in small-holder agriculture. So, both guilds would face the same fate because all crops on the farm receive insecticides either from direct spray or from drift.

We predicted that all three landscape complexity metrics would have a positive relationship with bee abundance and species richness, but only mean shape index was positively related while mean patch size and edge density did not. Here we used landscape complexity as a proxy for agricultural intensification where simple landscapes are generally more intensively managed compared to complex landscapes that are less intensively managed and have a mix of resources available for free-foraging organisms (Tschamtko et al. 2005). Species richness was not affected

by any complexity factor. The farming system in our study area is small-holder driven and farms are typically interspersed with semi-natural habitats across the landscapes producing mosaics of heterogeneous habitats.

From our findings, we propose the adoption of interventions such as organic farming that are by far more effective in sustaining healthy populations of important crop pollinators such as bees than conventional farming (Holzschuh et al. 2008, Allsopp et al. 2014). The practices used in organic farming support more pollinators than conventional farming (Holzschuh et al. 2008). For example, unlike conventional farming where bees are exposed to numerous toxic chemicals through a variety of routes, organic farming is characterised by reduced bee exposure to pesticides and other toxic chemicals. In addition, organic farming practices promote the existence of a variety of habitats within agricultural landscapes that provide habitat corridors and links between patches (Le Coeur et al. 2002). This is important for supporting higher bee diversity and could potentially benefit pollinators in our study system by enabling bees to forage for pollen from diverse sources across the landscape (Holzschuh et al. 2008; Power and Stout 2011, but see Sarospataki et al. 2009; Brittan et al. 2010a).

Pollination services

There was a significant decline in pigeon pea seed set when pollinators were excluded from flowers. The strongest relationships between fruit set and bee abundance were carpenter bees, social bees and solitary bees, which are among the most abundant bees visiting the flowers in this system. Although pigeon pea is self-compatible to some degree, recent cultivars released to farmers rely on bees and other insects for sufficient pollination, with bees effecting 70 % of out-crossings (Choudhary 2011). Bee species belonging to these guilds should be targeted for

conservation for this cropping system, and conservation strategies can be developed around the resources required by these bees, such as nesting suitable for carpenter bees. In addition, abundant floral resources should be available for colonies of social bees when the target crop is not in bloom in order to sustain the population. Insecticide application should be appropriately managed to mitigate effects on solitary bees.

No other study, to our knowledge, has examined legume crop pollination at local and landscape levels in-tandem in a tropical setting. Our findings provide the foundation for conservation efforts by identifying which bee guilds pollinated the crop. From our study, we suggest managing the floral and nesting resources that would best support the most abundant crop pollinators, and also reducing insecticide application to the crop. Further work will need to focus on more direct measures of bee visitation by guild to pigeon pea in controlled experiments to determine the independent and combined contribution of fruit set and to establish economic value. By identifying specific guilds to target for conservation, future efforts can examine the best way to manage resources required by particular bees. Targeted measures for conserving resources would not only sustain yields, but also benefit conservation of biodiversity and promote a sustainable agricultural system within this small-holder agricultural landscape.

Acknowledgments We are greatly indebted to the Felix Trust for funding this study through a Ph.D. scholarship at the University of Reading. We thank Mr. K. Wambua for his tremendous support with field work. Many thanks to Dr. C. Eardley and Prof. L. Packer for their great help with bee identification. Finally, we thank all the support from the National Museums of Kenya and the farmers of Kibwezi.

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