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Spatiotemporal changes in flying insect abundance and their functional diversity as a function of distance to natural habitats in a mass flowering crop

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ABSTRACT

To meet the dietary requirements of a burgeoning human population, the demand for animal-dependent crops continues to grow. To meet the demand, intensive farming practices are used. The gains in food production associated with agricultural intensification may be offset by its detrimental effects on pollinator populations through natural habitat fragmentation and pesticide use. Abundance and species richness of pollinators have been found to decrease with increasing distance to natural habitat in agroecosystems, reducing crop yields. A key aspect of crop pollination lies in the diversity of functional traits (functional diversity, FD) of flower-visitor communities within crop fields. Higher FD allows improved pollination success through complementarity between flower-visitors' morphology, phenology and behaviour. Many studies reported negative effects of increasing distance to natural habitats on the abundance and richness of flower-visitor communities, but the link between FD and natural habitat isolation is less well understood. Also, a more complete understanding of the functional traits of flower-visitor communities within crops should consider potential variations through time. Differences in resources availability between seasons are important in tropical areas and could modify ecological responses of flower-visitor communities to isolation. In this study, we surveyed the Hymenoptera and Diptera communities within mango orchards of South Africa using pan traps at 100 m, 200 m and at the maximal distance possible from any natural habitat. We measured the response of insect abundance, wing span and body size as well as functional diversity to habitat isolation during mango flowering (dry season), and during the wet season (after mango fruit harvest). Flying insect abundance decreased with increasing distance to natural habitat during mango flowering, but no effect was detected during the wet season. FD of flying insects declined with increasing distance to natural habitat in both sampling periods. Insects captured during mango flowering were smaller but had higher wing length/body length ratios than those caught during the wet season. This study highlights that mango orchards are more inhospitable for flying insects during mango flowering. This effect might be due to low palatability of mango flowers, or pesticide use in mango fields. In order to maintain a high FD of flower-visiting species, and reduce the detrimental effects of habitat isolation to ultimately ensure better crop pollination, we propose establishment of patches of resource-rich habitats combined with judicious use of pesticides within orchards.

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1. Introduction

To ensure nutritional security to a burgeoning human population, the demand for animal-pollinated crops is continually increasing (Eilers et al., 2011; Ehrlich and Harte, 2015). To meet this demand, agricultural production has intensified in recent decades through conversion of large areas to monocultures, with concomitant loss of natural and semi-natural areas, and increasing use of agrochemicals (Tscharntke et al., 2005; Kennedy et al., 2013). However, given the reported negative effects of agricultural intensification on pollinator populations (Kremen et al., 2002; Vanbergen et al., 2013), the benefits of intensification for animal-pollinated crop yield might be negated by ensuing pollinator loss (Garibaldi et al., 2011a; Leonhardt et al., 2013; Deguines et al., 2014). By pollinating crops, insects provide a critical ecosystem service estimated to be worth more than €153 billion worldwide (Klein et al., 2003; Gallai et al., 2008; Winfree 2008). The decline of pollinators owing to agricultural intensification therefore raises concerns for food security (Aizen et al., 2008; Garibaldi et al., 2011a) and highlights the need for sustainable agriculture that ensures agricultural production whilst conserving biodiversity (Garibaldi et al., 2015, 2016).

In agricultural landscapes, natural areas provide habitat for wild insects and constitute sources of flower-visitors for crops (Kennedy et al., 2013; Morandin and Kremen, 2013). Many flower-visitors, such as bees, are central place foragers and usually visit plants close to their nests (Cresswell, 2000). As distant resources are more energetically costly to visit than proximate resources, it is predicted that flowers isolated from natural areas will be less frequently visited (Schmid-Hempel et al., 1985; Schmid-Hempel and Schmid-Hempel, 1986; Steffan-Dewenter and Tscharntke, 1999). In croplands, species richness of flower-visitors, visitation rates, and pollination services all tend to decline with distance to natural areas (e.g. Ricketts et al., 2008; Carvalheiro et al., 2010; Garibaldi et al., 2011b). Whether or not flower-visitors disperse from natural habitats into the adjacent crop depends on many factors such as floral resource abundance, floral reward level or type of management (e.g., Kennedy et al., 2013). In this respect, pollinator functional traits can be key. Most studies on the effect of distance to natural patches of vegetation have not considered flower-visitor traits or their functional diversity (e.g. Ricketts et al., 2008; Farwig et al., 2009; Carvalheiro et al., 2010, 2012; Garibaldi et al., 2011b; but see Jauker et al., 2009; Williams et al., 2010; Benjamin et al., 2014). Yet traits such as flower-visitor body size are likely to affect pollination success as these traits can influence insect behaviour, foraging distances and pollen deposition (Hoehn et al., 2008). For example, foraging distance is primarily dictated by pollinator body size, and small flower-visitors will forage closer to their nests (Araújo et al., 2004; Greenleaf et al., 2007; Benjamin et al., 2014). Moreover, several studies have shown that functional diversity (FD) of flower-visitor communities enhances pollination by providing complementary pollination services, for example through niche partitioning of resource use in time and space (Fontaine et al., 2006; Hoehn et al., 2008; Albrecht et al., 2012; Fründ et al., 2013). Studying the effects of isolation from natural areas on traits and FD of flower-visitors can thus shed light on the factors which affect both crop pollination and the persistence of diverse flower-visitor communities in agro-ecosystems, informing effective land management strategies (Williams et al., 2010; Benjamin et al., 2014).

Temporal dynamics of agricultural landscapes are also important. Cultivated areas exhibit particularly large temporal variations in floral resources which could affect flower-visitor communities (Westphal et al., 2003). Mass flowering crops such as mangoes (*Mangifera indica* L., Anacardiaceae) constitute a super-abundant floral resource during a short period of time, representing a resource pulse for flower-visitors (Orford et al., 2015). The relationship between increasing distance to natural habitat and flower-visitor communities has been mostly explored during crop mass flowering (e.g. Holzschuh et al., 2011) but negative effects of distance on flower-visitors are likely to be stronger when the crop is not flowering, because only flowering weeds then provide resources in cultivated fields. Seasonal variation of wild floral resources and flower-visitor communities also contribute to temporal variation of agroecosystems. Spatiotemporal turnover in flower-visitor assemblages varies between and within years in temperate and tropical ecosystems (Oertli et al., 2005; Rollin et al., 2015; Samnegård et al., 2015), with temporal changes in abundance or even functional traits of flower-visitors varying because of food and nesting requirements (Tylianakis et al., 2005; Rollin et al., 2015). Flower-visitor assemblages might respond differently to agricultural perturbations in different seasons (Samnegård et al., 2015). For example, in tropical environments, resources are more scarce and patchily-distributed during the dry season relative to the wet season. Greater mobility may therefore be advantageous to crop flower-visitors during the dry season (see Samnegård et al., 2015).

To explore those questions, we studied the response of potential flower-visitors (hereafter referred to as “flying insects”) to increasing distance from natural vegetation in mango orchards in north-eastern South-Africa in two different seasons. Mango is one of the most important tropical fruits produced in the world, and is economically important for income and employment-creation in the region (FAO, 2010). Research conducted in our study area in the past has found clear effects of distance on pollination (Carvalheiro et al., 2010, 2012), pest control (Henri et al., 2015) and bird assemblages (Ehlers Smith et al., 2015).

We used pan-traps to survey flying insects during mango flowering in the dry season (winter), and during the wet season (summer, when mango is not flowering), along transects of increasing distance to natural habitat. We hypothesised that the number of flying insects caught in traps would decrease with distance to natural vegetation. If isolation from natural areas is the only cause of the decrease in flying insect abundance, the effect should be consistent between seasons. We also measured wing span and body length of each flying insect and investigated distance effects on flower-visitor functional-trait diversity. We hypothesised a decline of the FD with increasing distance from natural areas in both seasons, since species loss caused by isolation is likely to result in loss of trait diversity. Finally, given links between size and flight abilities, we predicted that average insect body size would be larger with increasing distance to natural area.

2. Materials and methods

2.1. Study site

Our study site was situated in the Kruger to Canyons Biosphere Region, Limpopo Province, South Africa. This region includes agricultural areas and also two large protected areas (Kruger National Park and Blyde River Canyon reserve; 24° 24′S 30°50′E). The entire area retains more than 50% of intact vegetation unaffected by anthropogenic perturbations (Coetzer et al., 2013).

Other than tourism, agriculture is an important source of employment in the area. Although in some areas, there are small subsistence farms, in our study area, the farms are composed of sets of large blocks of monoculture stands of mango, citrus or avocado. Mango farms consisted of multiple plots of 0.66–3 ha (mean ± sd = 1.39 ± 0.87) separated by windbreaks of tall *Casuarina* sp. trees. All the study farms provided similar water and nutrient supply and made intensive use of herbicides (e.g., glycophosphates) and insecticides (neonicotinoids or organophosphates). The sets of blocks of mango plantation are bordered by patches of natural vegetation that vary in size, but are usually at least 250 m wide. These patches of natural vegetation have not been ploughed, and differ from natural vegetation in neighbouring Kruger National Park in that livestock have replaced wild herbivores. The vegetation in the area is Granite Lowveld (Mucina and Rutherford, 2006), a savannah in which the woody component is dominated by *Acacia (Senegalia) nigrescens* and *Sclerocarya birrea,* with a herbaceous layer that includes *Digitaria eriantha, Panicum maximum* and *Aristida congesta*.

The primary flower-visitors to mango in this area include Diptera (mostly Calliphoridae and Empididae families), and Hymenoptera (*Apis mellifera, Ceratina* spp. bees and species of *Campenotus, Monomorium* and *Tetramorium* ants; Carvalheiro et al., 2010, 2012). Mango is self-compatible, but only to a small extent: a bagging experiment found that there was 21% fruit set for inflorescences from which pollinators had been excluded (100% of fruit set in open inflorescences see Carvalheiro et al., 2010). Mango flowers do produce nectar, but only a small amount of pollen (Eardley et al., 2007).

The first surveys were performed during mango flowering (July–August 2013, dry season hereafter), with maximum temperatures averaging around 26 °C and minima of 9 °C. The lack of rain during this time means that few flowering species are in bloom for flower-visiting insects. We selected five mango farms separated from each other by between three to thirteen kilometres. Within each farm, we established two transects perpendicular to the edge between mango and natural vegetation. Along each transect, we sampled insects at 5 sampling points, at 50 m from the edge with mango in the natural vegetation, at the field edge (0 m) and at 100, 200 m and the maximal distance possible from any natural habitat within mango orchards. Distance to natural vegetation was measured as the distance from each set of traps within the blocks of mango to the border of the nearest patch of natural vegetation. During April–May 2014, we re-sampled insects in two transects in each of the three most accessible farms. April–May coincides with the end of the wet season, when maximum and minimum temperatures average 29 °C and 12 °C, respectively, and floral resources are fairly abundant, having flourished during the rains.

At each sampling point, three coloured pan traps (radius = 7.25 cm, depth = 5 cm) painted with UV-reflecting paints (yellow, blue and white) were placed and filled with 400 ml of water and a drop of detergent (surfactant). Although pan trap sampling is known to under-sample some insect groups like large bees (*Bombus*, *Colletes*), this method is nevertheless considered the most efficient method to sample flying flower-visitors (Roulston et al., 2007; Westphal et al., 2008; Nielsen et al., 2011). It allows sampling of a large number of points simultaneously and uniformly, obtaining standardized estimates of flower visitor abundance and diversity.

2.2. Data collection

In dry and wet seasons, we performed three sampling sessions in each transect (one every two weeks) where traps were set out in the field for 24 h before being collected (N = 720 pan traps). Traps were set on warm sunny days (minimum of 15 °C, no wind and clear sky). Once collected, insects were stored in 70% ethanol before being rinsed, identified at the order level and measured. We focused on potential pollinators including Hymenoptera, Lepidoptera and Diptera, which are groups that are considered as mango pollinators (Sung et al., 2006). Morphometric measures of insects were also taken, *i.e.* wing length (distance between the wing tips) and body length using digital callipers (Digit-Cal MK IV 599-571, Brown and Sharpe, USA, 0.01 mm).

Finally, we assessed the number of mango flowers and wild flowers in a perimeter of 15 m around each sampling point. Within mango orchards, the herbaceous cover was dominated by non-native weeds (*e.g. Tridax procumbens* (L.) and *Bidens pilosa* (L.), both Asteraceae). Since mangoes exhibit “big bang” flowering with a massive number of flowers per tree, we estimated the number of mango flowers by counting the number of flowers on three different panicles and multiplying the average by the number of panicles for each tree (a mature tree has 600–1000 panicles; Manning, 1995; Sung et al., 2006).

2.3. Functional diversity

Our dataset was comprised of individual insects, and not species, so we calculated functional diversity of the individuals found in our samples. We used order, body length, wing span and the ratio of body length to wing length as traits. Order was represented as a binary variable of one or zero for each of three categories (Diptera, Hymenoptera or Lepidoptera), and therefore order was represented by three “traits”. We therefore down-weighted order to one third the value of the other traits to avoid biasing the analysis.

We calculated the FDis (Functional Dispersion, Laliberté and Legendre, 2010) measure of functional diversity, using the FD package in R (Laliberté et al., 2010). In this case, FDis is the mean distance of individuals to the centroid calculated for all individuals in multidimensional trait space. FDis is not affected by species richness (in our case, abundance), and is able to handle missing values and qualitative as well as quantitative traits (Laliberté and Legendre, 2010).

2.4. Data analysis

We assessed how functional diversity and the value of each of the traits used to calculate functional diversity (i.e. body length, wing length, and ratio of wing length over body length) changed with season and habitat. Although functional diversity is a measure of the variation in these traits, changes in the average values of traits yields insights into how the traits themselves are affected by habitat and season. These two analyses therefore produce complementary information.

We assessed the effects of sampling season (dry or wet season), habitat (natural vegetation or mango fields) and distance to natural habitat, as well as the interactions between season and distance or habitat effects, on flower abundance, abundance and traits of flying insects and on flying insect functional diversity. To do so, for each response variable, we performed a model averaging approach which allows comparison of all possible submodels from a global model containing all the predictors of interest, in order to identify the best set of models describing the observed variation (Grueber et al., 2011). With this approach, it is possible to account for model uncertainty and to assess the relative importance of various predictor variables.

To analyse patterns in flower abundance, traits of flying insects and functional diversity FDis, we used linear mixed-effect models on log-transformed response variables (except for FDis) using distance to natural vegetation, sampling season, type of habitat, interactions between distance and sampling season, and interactions between type of habitat and sampling season as fixed variables. Farm, transect nested within farm and date of sampling were included as random effects to avoid pseudo-replication (Crawley, 2007). Additionally, in models with insect traits as a response variable, we included insect order as a random effect to account for differences in trait values between orders.

To assess variations in abundance of flying insects, we carried out generalized linear mixed-effect models (GLMER) with a Poisson distribution and a log-link using the same fixed and random variables with the addition of flower abundance as a fixed variable. We included flower abundance as an explanatory variable because pan-traps are known to be less attractive to flower-visitors in resource-rich sites relative to resource-poor sites (Wilson et al., 2008). The GLMERs were corrected for overdispersion by including observation-level random factors (Harrison and Winfree, 2015).

For each response variable, we selected the set of models according to the Akaike information criterion (AIC). More precisely, we kept the models that were within the range of four highest AIC units and we used these “top models” to estimate the mean effects and confidence intervals of each predictor variable using model averaging (natural average method, Grueber et al., 2011). We also measured the relative importance of each predictor variable which is expressed as the relative sum of the Akaike weights across all top models in which the variable appears (relative importance is equal to 1 for variables present in all top models). Additionally, we calculated the marginal R^2 values (fixed effects) and conditional R^2 values (R^2 both fixed and random effects) to assess the amount of variance explained by the best model (i.e. with highest AIC; Johnson 2014). All analyses were performed using the R statistical interface (v 3.1.0, R Development Core Team, 2014); mixed models were conducted using the package lme4 (Bates et al., 2014) and model comparison and averaging were performed with the functions dredge, get.models and model.avg (package MuMIn; Barton, 2016). Model predictor variables were also centered and standardized with the function standardize (package arm; Gelman and Su, 2015) to facilitate comparison between the relative strengths of parameter estimates (Grueber et al., 2011). R^2 values were calculated with the function r.squared GLMM (package MuMIn; Barton, 2016).

3. Results

3.1. Abundance of flowers

Distance to natural vegetation, as well as habitat type, sampling season and their interactions (habitat × season and distance × season), were included in all top models describing the response of flower abundance (Table 1). As expected, the abundance of flowers was greater in mango fields in the dry than in the wet season, whereas we observed more flowers in the nearby natural vegetation during the wet season (see parameter estimate and confidence interval of the interaction between sampling season and habitat type in Table 1, Fig. 1A). Flower abundance was far higher in the mango fields than in the natural vegetation during the dry season (Fig. 1A), given that we did not observe any flowers in the neighbouring natural vegetation in any of the sampling sessions in the five farms over the dry season. The abundance of flowers also increased with increasing distance from natural vegetation (Fig. 1A). The interaction between distance and season had only 35% relative importance to other predictor variables and the confidence interval for this parameter estimate included 0. Thus there was little evidence that the effect of distance from natural vegetation on flower abundance differed between seasons.

3.2. Abundance of flying insects

Distance to natural vegetation, sampling season, and the interaction between these two variables, were included in all top models describing the response of abundance of flying insects (Table 1). The abundance of flying insects was far higher during the wet season than the dry season, which was expected since we captured 798 insects in the five farms during the dry season but captured 1719 insects in only three of these farms during the wet season. Abundance of flying insects declined with increasing distance from natural vegetation, but only during the dry season (Table 1, Fig. 1B). The difference in abundance of flying insects between the two sampling periods was also more pronounced in mango fields (see parameter estimate and confidence interval of the interaction between sampling season and habitat type in Table 1), but there was weaker evidence for this effect (55% relative importance). Lastly, there was very little evidence of an effect of flower abundance on the abundance of flying insects (39% relative importance to distance and season, and the confidence interval for this parameter estimate included 0).

3.3. Functional diversity

Distance to natural vegetation and sampling season were included in all top models describing the response of functional diversity (Table 1). Functional diversity of flying insects was higher in the wet season than during the dry season and FD declined with increasing distance from natural vegetation in both seasons (Fig. 1C). Functional diversity was also higher in nearby natural vegetation than in mango fields (79% relative importance to distance and season, Table 1). The interaction between distance and season had only 23% relative importance and the confidence interval for this parameter estimate included 0. Thus, there was

Table 1

Model selection for flower abundance, insect abundance and functional diversity. N corresponds to the number of models selected in the top 4AIC_c, R^2_m and R^2_c correspond respectively to the marginal and conditional R^2 values of the best model. Est. corresponds to the parameter estimate (for centralized and standardized predictor variables), CI to its 95% confidence interval and Imp. to the parameter relative importance. * Mango field was the reference habitat and § the dry season was the sampling season of reference.

	Flower abundance (N = 2 models)			Insect abundance (N = 6 models)			Functional diversity (N = 6 models)		
	R^2_m = 0.40; R^2_c = 0.68			R^2_m = 0.54; R^2_c = 0.67			R^2_m = 0.32; R^2_c = 0.41		
Parameter	Est.	CI	Imp.	Est.	CI	Imp.	Est.	CI	Imp.
Intercept	2.867	(2.056, 3.679)		1.402	(1.120, 1.683)		0.069	(0.059, 0.082)	
Habitat*	−2.563	(−3.033, −2.093)	1.00	0.255	(−0.082, 0.592)	0.68	0.017	(0.0002, 0.033)	0.79
Season§	−1.427	(−1.756, −1.098)	1.00	1.393	(1.033, 1.751)	1.00	0.048	(0.033,0.063)	1.00
Distance	0.538	(0.187, 0.889)	1.00	−0.632	(−0.940, −0.325)	1.00	−0.026	(−0.042, −0.011)	1.00
Habitat × Season	2.363	(1.632, 3.093)	1.00	−0.517	(−0.962, −0.072)	0.55	0.015	(−0.007, 0.038)	0.45
Distance × Season	0.326	(−0.346, 0.999)	0.35	0.687	(0.227, 1.148)	1.00	−0.006	(−0.036, 0.023)	0.23
Flower abundance				−0.119	(−0.328, 0.089)	0.39			

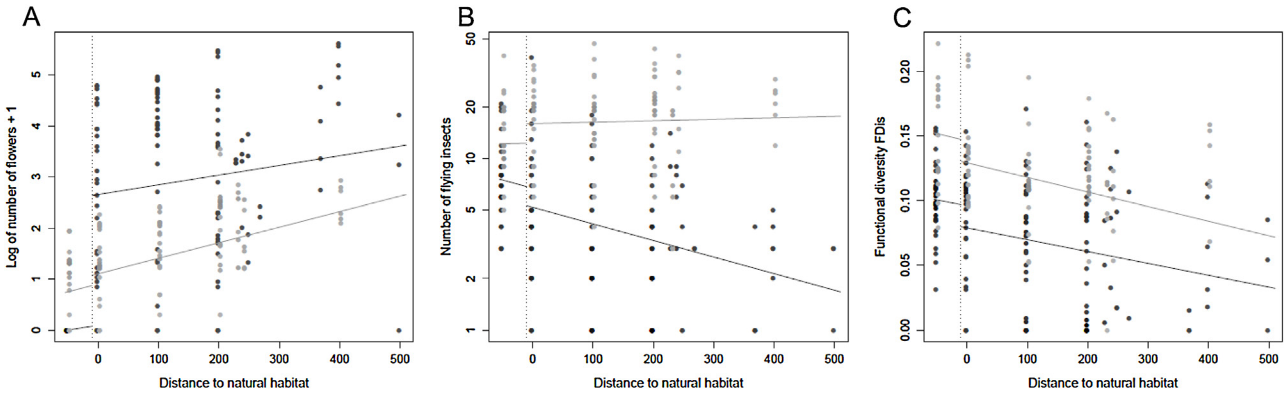

Fig. 1. Effect of distance to the natural habitat (m), habitat type and sampling period on: A. abundance of flowers (log + 1), B. abundance of insects, and C. functional diversity of insects. Lines represent model predicted values. In all panels, mango flowering period (dry season) is represented in dark grey and mango non-flowering period (wet season) is represented in light grey.

little evidence that the negative effect of distance from natural vegetation on functional diversity differed between seasons.

3.4. Insect traits

Only sampling season was included in all top models describing the responses of body length, wing span and ratio of wing span to body length of flying insects (Table 2). Both body length and wing span of flying insects were on average smaller during the dry than during the wet season, whereas the ratio of wing span to body length was larger during the dry season (Fig. 2). Body length and wing span of flying insects also differed between habitat types, insects being on average larger in natural vegetation than in mango fields (Fig. 2, Table 2). Although body length and wing span of flying insects tended to decrease with increasing distance to natural vegetation during the dry season (Fig. 2), this effect was not significant (the confidence interval for the corresponding estimate included 0). There was very little evidence of any effect of habitat type and distance to natural vegetation on the ratio of wing span to body length of flying insects (Table 2). In addition, the marginal R^2 of the models were very low (about 0.02, see Table 2), indicating that on average variance in insect traits explained by effects of distance, habitat type and sampling season was only 2% whereas random factors (which represented insect order, as well as sample position and date) explained between 40 and 50% of the variation.

4. Discussion

This study highlights that mango orchards are more inhospitable for flying insects during the dry (mango flowering) than during the wet season, despite the abundance of mango flowers available in the orchards. We found declines in insect abundance with increasing distance to natural areas during the dry season whereas no pattern was found during the wet season. The functional diversity (FD) of flying insects declined with increasing distance to natural habitat in both sampling periods, however, and insects were on average smaller in mango orchards than in natural vegetation. Taken together, our results suggest impacts on crop yield, given that as a rule, rate of flower visitation (Vázquez et al., 2005; Garibaldi et al., 2013) and functional diversity (Fontaine et al., 2006; Hoehn et al., 2008; Albrecht et al., 2012; Fründ et al., 2013) increase crop fruit set. Creating patches of habitat rich in native floral resources that flower before and during mango flowering within orchards could mitigate the detrimental effects of isolation from natural habitats and increase mango production (Carvalheiro et al., 2012).

4.1. Seasonal variation in flying insect abundance

Agricultural landscapes show strong temporal variation in the floral resource offer. Mass flowering crops, during their flowering season, are expected to exert a strong magnet effect on pollinators from adjacent areas (Blitzer et al., 2012). We did not find this effect, however, and this was somewhat surprising, given that there are few other floral resources in the landscape at this time. It is possible that this pulse of floral resources is too short-lived to enable invertebrate populations to respond to this sudden availability in floral resources. This finding highlights the importance of considering seasonal variation in the value of agricultural patches for pollinators.

The decline in insect abundance with increasing distance to natural vegetation that we observed during the dry season is a

Table 2
Model selection for body length, wing span and ratio of wing span over body length. Same legend as Table 1. * Mango field was the reference habitat and § the dry season was the sampling season of reference.

	Body length ($N = 7$ models)			Wing span ($N = 7$ models)			Ratio of wing span over body length ($N = 5$ models)		
	$R^2_m = 0.037$; $R^2_c = 0.45$			$R^2_m = 0.015$; $R^2_c = 0.54$			$R^2_m = 0.02$; $R^2_c = 0.40$		
Parameter	Est.	CI	Imp.	Est.	CI	Imp.	Est.	CI	Imp.
Intercept	0.556	(0.271, 0.840)		0.805	(0.433, 1.177)		0.248	(0.155, 0.342)	
Habitat*	0.049	(0.0007, 0.097)	0.89	0.052	(0.006, 0.099)	0.93	−0.0004	(−0.013, 0.013)	0.24
Season§	0.168	(0.112, 0.225)	1.00	0.126	(0.067, 0.186)	1.00	−0.042	(−0.061, −0.022)	1.00
Distance	−0.047	(−0.109, 0.014)	0.68	−0.018	(−0.095, 0.028)	0.52	0.002	(−0.011, 0.015)	0.28
Habitat × Season	−0.023	(−0.10, 0.053)	0.32	−0.008	(−0.097, 0.048)	0.32	0.003	(−0.019, 0.025)	0.07
Distance × Season	0.060	(0.004, 0.117)	0.53	0.016	(−0.011, 0.109)	0.32	−0.009	(−0.028, 0.009)	0.10

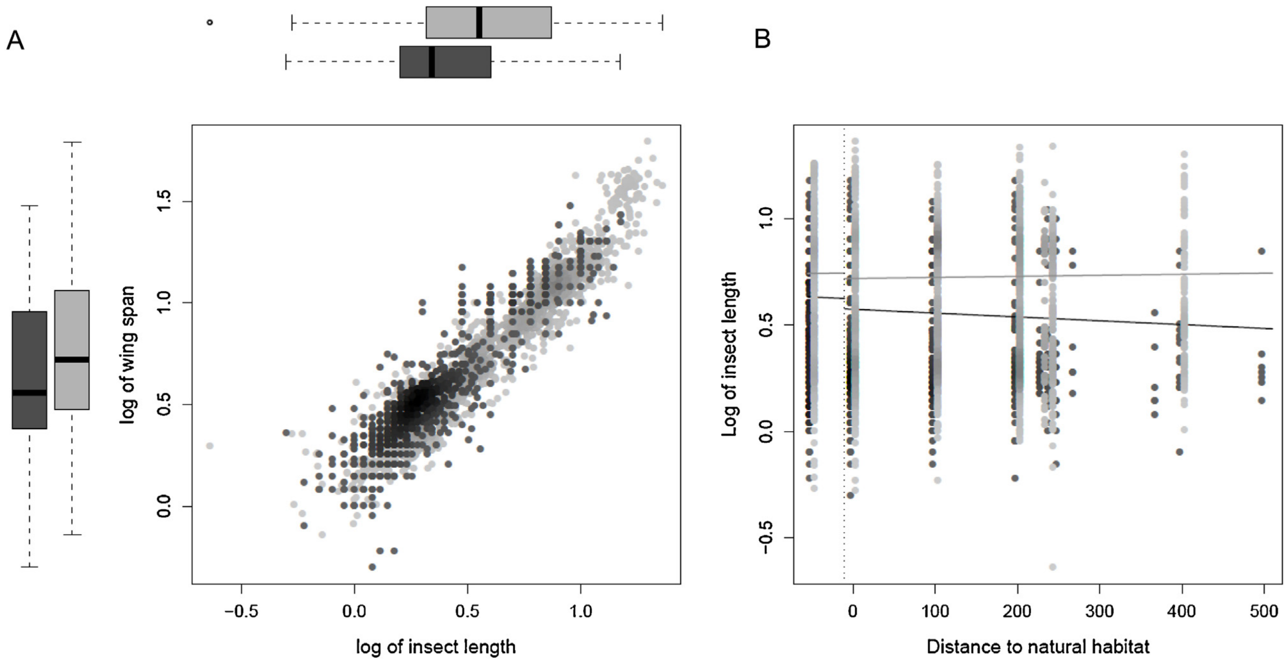

Fig. 2. Relationship between body length (mm) and wing span (mm) of flying insects (A), and effect of distance to the natural habitat (m) and habitat type on insect body length (B). Mango flowering period (dry season) is represented in dark grey and mango non-flowering period (wet season) is represented in light grey.

pattern that has been observed in numerous studies in agricultural systems (*e.g.* Ricketts et al., 2008; Garibaldi et al., 2011b). This pattern appears stronger in tropical than temperate regions (Ricketts et al., 2008) and has been particularly well documented by Carvalheiro et al. (2010) in our study system. This latter study notably showed that even in a biodiversity rich area, with a high proportion of intact natural habitat, the abundance of flying insects was impacted by isolation from natural habitats, which in turn impacted crop fruit set. Because several flying insects such as bees are central place foragers *i.e.* individuals that return to their nests after foraging (for nectar and/or pollen; Williams and Kremen, 2007), this decline in insect abundance with increasing distance to natural area is commonly attributed to the distance from nesting sites and foraging resources available in natural habitats (*e.g.* Ricketts et al., 2008; Farwig et al., 2009; Williams et al., 2010; Garibaldi et al., 2011b; Samnegård et al., 2015).

But intriguingly, in complete contrast to the dry season when mango is flowering, we did not observe any effect of distance to natural area on insect abundance during the wet season. These contrasting results might be explained by the seasonal dynamics of wild floral resources and pollinator communities. Flying insects were more abundant and had higher functional diversity during the wet than dry season, which is expected since the wet season coincides with spring/summer, when more floral resources are available and temperatures are higher. The link between plant richness and abundance and flower-visitor richness and abundance has been well documented in the scientific literature for croplands (*e.g.*, Holzschuh et al., 2007; Kennedy et al., 2013). The higher diversity of native flowering plant during the wet season, and the increasing availability of weed flowers with increasing distance from natural vegetation within mango orchards might explain the absence of a relationship between isolation from natural habitat and insect abundance. It is also worth noting that mango flowers yield only small amounts of pollen, although they do offer some nectar (Eardley et al., 2007), and so are not very attractive to many, insects (Free and Williams, 1976). Thus, the lack of attractiveness of mango mass flowering might explain the strong negative effect of isolation from natural habitat we observed during the dry season. This idea is supported by an earlier study in which small planted patches of native flowering plants within mango orchards were associated with an increased abundance of flower-visitors to mango flowers, which mitigated to some extent the effects of isolation (Carvalheiro et al., 2012).

In addition to the limitations in floral resources, alternative explanations exist that might explain seasonal variation in distance effects on flying insects in the crop. Pesticides are used in mango fields, even during mango flowering. Many studies have reported on the negative effect of pesticides on flower-visitors (Henry et al., 2012; Goulson et al., 2015; Stanley et al., 2015), and Carvalheiro et al. (2012) also previously highlighted the detrimental effect of pesticide use on flying insect along gradients of increasing distance to natural area in our study system. Varying pesticide applications might thus also explain the different effects of distance to natural area on insect abundance between the two sampling seasons.

Pan-traps are widely considered to provide accurate surveys of bee assemblages (Roulston et al., 2007; Westphal et al., 2008; Geslin et al., 2016), but are also prone to some bias. Pan-traps under-sample large insects and their attractiveness can vary with the amount of flowers locally present (Wilson et al., 2008; Popic et al., 2013). The relative attractiveness of pan-traps decreases as floral resources increase because pan traps compete with flowers for flying insect attention. However, it is unlikely that our results are an artefact of pan-trapping. We included floral abundance as an explanatory variable in our statistical models, and this variable did not have a significant effect on insect abundance. Secondly, in both seasons, more flowers were observed in mango orchards compared to natural habitats and the decline in insect abundance with increasing distance to natural habitat was observed uniquely during the dry season, with the same capture method.

4.2. Functional diversity

Although flying insect abundance decreased with increasing distance from natural habitat during the dry season only, declines in functional diversity with increasing isolation were consistent in the two sampling seasons. A recent study highlighted that farmed landscapes were detrimental to the maintenance of functional-trait diversity of flying insects (Forrest et al., 2015), and our findings support this view.

FD is increasingly recognized as being more important than species diversity to ecosystem functioning (Gagic et al., 2015) and has been suggested to be the major component of diversity (Tilman et al., 1997; Hulot et al., 2000; Hoehn et al., 2008). The main reason for the importance of FD lies in the complementarity of pollination services through niche partitioning of resource use in time and space (Fontaine et al., 2006; Hoehn et al., 2008; Albrecht et al., 2012; Fründ et al., 2013). The value of greater FD to pollination services has been demonstrated both experimentally (Fontaine et al., 2006) and empirically (Hoehn et al., 2008), and a recent example in apple orchards highlighted that fruit and seed set was mainly mediated by bee FD (Martins et al., 2015; but see Garibaldi et al., 2015).

The loss of FD with increasing isolation can reduce the efficiency of pollination (Forrest et al., 2015; Wood et al., 2015) reducing yield for trees at the centre of mango orchards. Carvalheiro et al. (2010, 2012), demonstrated that agricultural production and proximity to natural habitat are positively correlated in the mango orchards we studied. Yet, easily implementable management practices might ameliorate, to some extent, the negative effects of isolation. Creating patches of flowering rich habitat has been shown to increase crop yield in mango orchards (Carvalheiro et al., 2012). FD of flying insects has been shown to improve with only modest enhancements of floral diversity (Orford et al., 2016). Given that isolation from natural habitat together with loss of flower-visitor abundance and diversity are now well established as critical drivers of limitation in crop yield (Garibaldi et al., 2016), we encourage the establishment of those simple management practices to enhance food production.

4.3. Traits of flying insects

In contrast to functional diversity, there was weak evidence of distance effects on average insect trait values, and the traits were only weakly affected by habitat type. Although a large part of the variance in insect traits was related to size differences between orders, sampling season had also a significant effect on flying insect average body length and wing span.

During the dry season in tropical environments, resources are scarcer and more patchily-distributed compared to the wet season (Samnegård et al., 2015). Because the foraging range of flying insects is positively correlated with their body size (Araújo et al., 2004; Greenleaf et al., 2007), we initially hypothesized that we would trap larger flying insect during the dry season. However, our results show that insects were smaller during the dry season. This finding is more consistent with the findings of Wray et al. (2014), who found large-bodied species to be favoured by increasing availability of floral resources (although this was in a landscape context of urbanisation). Indeed, large-bodied species may have larger resource needs and smaller population sizes (Kremen and M'Gonigle, 2015), which could disadvantage them during the dry season. We nevertheless did detect a greater ratio of wing to body length during the dry season, which might indicate greater mobility of insects relative to their size than during the wet season. Insect size differences between seasons might also arise from differences in climatic conditions such as temperature. Some studies reported that higher wing to thorax size ratios could be selectively advantageous at lower temperatures (*e.g.*, Azevedo et al., 1998), which is in agreement with what we found during the dry/winter season.

Species turnover between seasons likely explains the difference in insect sizes between seasons. The distribution of insect body size/tongue size has been found to closely match the distribution of flower corolla tube depth (Agosta and Janzen 2005; Stang et al., 2006, 2009) and to determine the abundance of interactions in pollinator webs (Stang et al., 2006; Geslin et al., 2013). The distribution of the size of insects might be due to the predominance of flowers with short corollas during the dry season because mango flowers, as well as the dominant non-native weeds *T. procumbens* and *B. pilosa* have short corollas. This is supported by the fact that the few large individuals of flying insect we found during the dry season were trapped in natural habitat where plants such as *Grewia* spp., have flowers that present a more tubular and deep corolla structure. Finally, we observed larger insects, in both seasons, in the natural vegetation compared to mango orchards. Some studies have found large-bodied flying insects to be more prone to extinction in response to land use intensity and habitat loss (Larsen et al., 2005; Bartomeus et al., 2013; Rader et al., 2014), whereas others have found non-significant effects (Williams et al., 2010), and several authors found small insects to be more negatively affected by isolation and habitat loss than larger ones (Bommarco et al., 2010; Öckinger et al., 2010; Jauker et al., 2013). Here, large-bodied species seemed more sensitive to agricultural perturbations than small bodied ones and were thus less abundant in mango orchards. Moreover, flowers within mango orchards may be less attractive to large bodied insects because of the nectar and pollen offerings of mango flowers relative to wild flower species.

5. Conclusion

Our study provides new evidence of the detrimental effects of isolation from natural habitats, even in a biodiversity rich area, on abundance and functional diversity of flying insects in different seasons. Although these deleterious effects were season-dependent for insect abundance (i.e. negative effects of distance from natural vegetation only during crop flowering), functional diversity declined consistently with increasing distance from natural habitat in both dry and wet seasons. This study thus sheds a light on the importance of providing patches of resource-rich habitat within orchards over the year to mitigate the detrimental effects of isolation and maintain functionally-diverse insect communities. Such management practices are easily achievable in mango orchards and should be encouraged. Finally, this study also underlines the temporal variability within a year of patch use by flying insect communities within an agricultural landscape. Agricultural landscapes and mechanisms that structure flying insect communities should thus be studied at various spatial and temporal scales. We encourage new studies regarding links between morphological traits of insects and agricultural intensification, contributing to a synthesis that can untangle the relative importance of temporal and spatial contexts, crop and management practices.

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