Research Paper

Exotic plants growing in crop field margins provide little support to mango crop flower visitors

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ABSTRACT

Introduced plant species integrate into native trophic networks, often disrupting flower-visitation patterns. Although non-native invasive plants frequently occur in disturbed natural vegetation bordering crop fields, their impact on crop pollination has not been studied. We investigated whether an invasive plant (*Lantana camara*) influences flower visitation to mango (*Mangifera indica*), a pollinator-dependent crop, and whether the invasive supports mango pollinators when mango is not flowering. We surveyed insect flower-visitation in mango orchards bordering natural vegetation and within adjacent natural vegetation, with and without *L. camara* present, before, during and after mango flowering. We used these data to calculate the indirect effect of *L. camara* on mango through shared flower visitors before, during and after mango flowering, and the effects of the invasive on crop productivity. *Lantana camara* had a positive effect on mango flower visitation at low to medium mango flower density, but not at high mango flower densities. Although *L. camara* and mango shared flower visitor species, the frequency with which these flower visitor species visited the crop and the invasive differed markedly before, during and after mango flowering. Furthermore, the potential indirect effect of *L. camara* on mango via shared visitors was greatest when mango was flowering, but significantly lower before and after mango flowering, suggesting that the invasive is unimportant in the diet of mango flower visitors when the crop is not flowering. Contrary to findings in previous studies using native species in mango fields, there was a trend (not significant) for lower mango fruit production in fields with *L. camara*. This suggests that *Lantana* does not contribute to an increase in successful pollination of mango. Although our focal alien invasive plant species facilitated flower visitation of crops, it had no effect on mango production, and provided little support to mango flower visitor species that live longer than the crop's flowering period. Given that *L. camara* is detrimental to grazing and was not associated with increased mango production, the removal of this invasive is advisable.

1. Introduction

Non-native (alien) species can integrate into native plant-flower visitor networks (Carvalheiro et al., 2008; Lopezaraiza-Mikel et al., 2007). When invasive, these species can shrink natural capital, compromise ecosystem stability and endanger economic productivity (Pejchar and Mooney, 2009; Richardson and van Wilgen, 2004). The presence of invasive alien plants on pollination networks can have negative (competition), positive (facilitation) or neutral effects on flower visitation to native plant populations (Bartomeus et al., 2008; Lopezaraiza-Mikel et al., 2007; Memmott and Waser, 2002; Morales and Traveset, 2009; Vilà et al., 2009; Hansen et al., 2017), and hence influence pollination success of natural flora.

Natural vegetation borders crop fields, and this natural habitat can support crop pollinators (Carvalheiro et al., 2010; Geslin et al., 2016) and predators of crop pests (Ehlers Smith et al., 2015; Henri et al.,

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2015; Morgan et al., 2016; Moxley et al., 2017). Invasive alien plants are often found in the disturbed margins on the edges of crop fields (Vardien et al., 2012), however. These species can integrate into pollination networks, luring pollinating insects away from crops (Potts et al., 2003), potentially posing a risk to crop pollination (Cook et al., 2007). Alternatively, they may attract insects, or support crop flower visitors when the crop is not flowering, and thus facilitate crop pollination. The demand for animal-pollinated crops, which represent approximately 35% of the world's crop production, is increasing (Aizen et al., 2009; Klein et al., 2007), so a broad understanding of factors influencing pollinator assemblages within agricultural systems is needed (Burd, 1994; Free, 1970). Little work has been done to date on the effects (facilitative or competitive) of invasive plant species on pollinator-dependent crops, which are often also introduced species.

Mango (*Mangifera indica*) is an important crop worldwide which requires insect pollinators for good seed and fruit set; previous work has shown that exclusion of flying and crawling flower visitors is associated with a 79% decrease in fruit set (Carvalheiro et al., 2010). Several alien plant species (e.g., *Lantana camara*, *Melia azedarach*, and *Bidens pilosa*) have become well-integrated into pollination networks in the Limpopo area, north-eastern South Africa (Carvalheiro et al., 2010), and it is possible that these invasive species could facilitate or compete with crops for pollinators.

Lantana camara (hereafter referred to as *Lantana*) is an aggressive weed originating from Central and South America that has invaded many areas of South Africa where mango plantations occur (Vardien et al., 2012). It has adverse effects on natural ecosystems and native plant species diversity (Vardien et al., 2012), forming large stands, often along the boundaries of agricultural land and nearby natural vegetation (ARC, 2010).

Mango and *Lantana* share floral characteristics: both species' flowers produce nectar, occur in inflorescences with small (diameter < 5 mm) whitish to pink flowers (although *Lantana* can also have yellow flowers), and have been found to share honey bees as flower visitors (Carvalheiro et al., 2010; Goulson and Derwent, 2004). The concentrations of nectar in the two species are comparable: mango at around 48% (Kajobe, 2007), *Lantana* at around 38% ± 9.4%; (Hainsworth et al., 1991). These shared characteristics may increase the possibility of interactive effects between the two plant species (Bjerknes et al., 2007). Thus, where *Lantana* and mango coexist, they could compete with or facilitate each other for pollinators.

This study makes use of the presence of *Lantana* near to mango crop fields to test whether invasive alien plants affect crop pollination. Given that previous studies show that mango visitation benefits from the presence of other floral resources (e.g. *Aloe greatheadii* and *Barleria obtusa*, see Carvalheiro et al., 2012), that *Lantana* has attractive floral attributes, similar floral traits to mango, as well as an extended flowering period (relative to mango) we expected this invasive plant to be associated with greater abundance and species richness of flower visitors to mango (hypothesis 1), that *Lantana* should share flower visitors with mango, supporting them outside mango flowering peak (hypothesis 2), and that the presence of *Lantana* would increase mango fruit production (hypothesis 3). Testing these hypotheses will allow us to determine whether there is any advantage for farmers to having *Lantana* present around the borders of mango orchards, which could help guide management practices.

2. Methods and materials

2.1. Study area and design

This study was conducted on three commercial mango farms near Hoedspruit, Limpopo Province, South Africa, within the Kruger to Canyons Biosphere Reserve (24°31′S 30°44′E). The natural vegetation is classified as Granite Lowveld (Mucina and Rutherford, 2011). The farms (Bavaria, Jonkmanspruit and Mohlatsi) share similar

management practices (i.e., pesticide application of neonicotinoids or organophosphates, cropping system, irrigation, in-field weed control and harvesting period), and abiotic conditions (climate, soil and sunlight exposure). Soil water and nutrient content, important variables in crop production, are monitored throughout the year to keep conditions optimal for mango production (J. du Preez and G. Schoeman *pers. comm.*), presenting minimal variation in abiotic conditions (details on farms given in Table A1, online Appendix). The farms are divided into blocks of mango trees, approximately 150 m × 70 m of a single cultivar, within a grid of non-native trees (*Casuarina* sp.) that serve as windbreaks. The blocks of mango are surrounded by natural vegetation, which is mostly undisturbed, intact vegetation. Although it has lost its indigenous wild herbivores, this vegetation is grazed by livestock, mainly cattle. The disturbance associated with clearing for mango farming has enabled the non-native *Lantana* to establish in parts of the natural vegetation, particularly areas bordering mango fields.

On each farm, we carried out monthly flower visitation surveys in twenty pairs of fixed observational plots from June to October 2013, a period that includes mango flowering season (July-August). Each pair of plots consisted of one plot in mango orchard bordering natural vegetation and another plot located within the bordering natural vegetation (ca. 15 m from one another, within natural vegetation areas > 200 m²; Fig. 1 shows the layout of these plots on one of the farms, Bavaria Estates, as an example). Ten of these pairs had *Lantana* present in the bordering vegetation, representing various densities of *Lantana*, the other ten bordered natural vegetation without *Lantana*. The pairs of plots were between 100 and 400 m apart from one another, and included five mango cultivars (i.e. Kent, Keitt, Sensation, Tommy Atkinson and Shelly; Table A1 in Online Appendix). All plots were at least 150 m away from large water bodies. Honey bees (*Apis mellifera scutellata* Lepeletier) are brought in to ensure pollination, although previous studies have found the presence of honey bee hives to have little influence on mango production (Carvalheiro et al., 2010). All sites in this study had managed honey bee colonies present during the mango flowering season (i.e., July–August), at densities of approximately one colony per hectare.

Fig. 1. Map showing paired observational plots on Bavaria Fruit Estate, where mango plots border natural vegetation with *Lantana* (white circles) and without *Lantana* (red circles). One such paired plot is depicted (bottom right) where the mango orchard border (yellow star) is near natural vegetation margin (red star) (Google Inc., 2014). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Flower visitation surveys

Flower visitors were surveyed before (June 2013), during (July–August 2013) and after (September–October 2013) mango flowering. Two observers stood at opposite points of a 2 × 2 m plot for 20 min to detect any flower-insect interactions in which the insect came into contact with flower stamens, potentially leading to pollen transfer. Each insect visiting a single flower was recorded as an individual flower visitation event, and any subsequent flower visitation to other flowers by the same individual in the observation plot were counted and recorded as separate flower visitation events. Plant species was noted and flower visitors sampled for later identification to morphospecies or species, if possible. We surveyed both ants and flying insects. Ants were included because they have been found to facilitate early mango fruit set, although not full fruit development (Carvalheiro et al., 2010). As mango anthesis is diurnal, visitation surveys took place between 08h00 and 16h00 on warm dry days (20–39 °C) with slow wind speed (0–4 km h^{-1}). Floral density (individual flowers per unit area) for all species other than mango was determined by counting the total number of open flowers, although flower heads were counted for species with composite flowers, like daisies. Naturally-occurring flowering plants (NOFPs) are considered to be any flowering plants (native or exotic spp.) present in the observational plots other than *Lantana* and mango (list provided in Table A2, online Appendix). Mango flower densities were estimated by averaging the total number of flowers counted on three random inflorescences and multiplying by the number of inflorescences within the observational plot.

2.3. Statistical analyses

2.3.1. Lantana's effect on mango flower visitor abundance and richness

To assess how mango flower visitor abundance and species richness were affected by the presence of *Lantana*, we used generalised linear mixed models (GLMMs) with Poisson distribution (log-link function). Fixed effects were mango floral abundance, the presence of *Lantana* (binary variable), distance between paired plots, and abundance (floral densities) of each of *Lantana* and NOFPs. To account for spatial and temporal autocorrelation, we included month, plot number nested within farm, and mango cultivar as random variables. All combinations of predictor variables and biologically-sensible two-way interactions were tested to determine the best-fit model. The best-fit model was identified as that with the lowest AICc value by 2 or more. AICc was used to correct for small sample sizes (Burnham and Anderson, 2002). GLMMs were constructed using the package lme4 and model selection was done using MuMIn in R (Bates et al., 2014; Burnham and Anderson, 2002; R Core Team, 2014). Variance explained by fixed effects and by fixed and random effects together (i.e., conditional and marginal R^2), were calculated for these random intercept models (Nakagawa and Schielzeth, 2013). Flower visitor – plant networks were constructed using the bipartite package in R (Dormann et al., 2009), to visually represent the difference in mango flower visitation with *Lantana* present or absent.

2.3.2. Support of mango flower visitors by Lantana

To ascertain whether *Lantana* supported mango flower visitors when mango was not flowering, we assessed the number of shared flower visitor species and their abundance, before (June), during (July–August) and after (September–October) mango flowering. We also assessed the number of visits per flower by mango flower visitors to *Lantana,* nofps, and mango, summed over the periods before, during and after mango flowering, using an ANOVA, to assess the relative importance of the three groups of plants to mango flower visitors. Given that different insect groups can show different flower preferences (Hegland and Totland, 2005; Simba, 2015), we assessed the relative proportion of visits made to mango and *Lantana* by flies, butterflies, beetles and bees.

We also calculated the overall contribution of *Lantana* to the diet of mango flower visitors before, during and after mango flowering, by assessing indirect effects. For each time period (before, during and after mango flowering), we pooled data for 10 pairs of the fixed plots (half containing *Lantana* in bordering vegetation, half without) on each farm to construct six flower visitor – plant networks. We pooled plot data to allow for sufficient visitation to enable detection of indirect effects. We then analysed these networks for potential indirect effects between flowering plants using Müller's index (Carvalheiro et al., 2014; Müller et al., 1999). Müller's index measures the relative potential effect that plant species *a* has on plant species *b,* and depends on the proportional contribution of plant *a* on shared flower visitors' diets. Müller's index is a value between zero and one, where zero signifies no indirect effect between two plants and a value close to 1 signifies the maximum indirect effect between two plants (i.e., complete dependency of plant *b* on plant *a*, if plant *a* contributes most to the diet of shared flower visitors of plant *b*). Müller's index was calculated using the PAC command in the bipartite package in R (Dormann et al., 2009; Müller et al., 1999).

Additional honey bees (*Apis mellifera*) are introduced to mango fields when the crop is in flower, to ensure pollination. This addition of managed pollinators complicates assessment and comparison of the supporting role of *Lantana* to crop flowers before, during and after mango flowering. Honey bees are indigenous to the area and therefore those visiting mango or *Lantana* during flowering could have been either managed or wild. However, previous studies found no significant effect of hive presence in mango flower visitation by honey bees (Carvalheiro et al., 2010), suggesting that most mango flower visitors come from wild colonies. In addition, there are also orchards for other crops in the vicinity, where additional honey bees might also be brought at different times of the year. To account for the addition of these managed pollinators, we therefore calculated Müller's index twice, once with, and then once without *A. mellifera* in the dataset. We then assessed whether the indirect effect of *Lantana* on mango differed before and after mango flowering relative to during mango flowering, first using indirect effects calculated with honey bees included and then indirect effects calculated with honey bees excluded. Given that Müller's index lies between 0 and 1, we used a two-limit tobit model in R, using the package VGAM (Yee, 2016).

2.3.3. Influence of Lantana on mango fruit production

We were able to obtain production data (kg mango/ha^{-1}) according to the blocks (n = 20) with which we worked for one of the three farms (Bavaria) on which this study was conducted. We used these data to assess whether mango fruit production differs according to the presence or absence of *Lantana* in neighbouring vegetation. We used a generalised linear model, with log (production (kg mango ha^{-1}) + 1) as the dependent variable, number of mango flowers in plots (summed for surveys before, during and after peak mango flowering) and presence of *Lantana* as fixed and mango cultivar as a random variable. We first tested for spatial autocorrelation using a Mantel test (9999 permutations) in the ade4 package (Dray and Dufour, 2007), and then determined the best model as for Question 1.

All model assumptions (patterns in deviance residuals and lack of fit) were checked and satisfied during model validation.

3. Results

Floral density of *Lantana* was more constant throughout the study period than that of mango (*Lantana* flowers per plot: $\bar{x}$ = 1031, SD = 467; Mango flowers per plot: $\bar{x}$ = 8978, SD = 6294; Fig. 1). NOFP floral densities were one to two orders of magnitude lower than that of *Lantana* and mango ($\bar{x}$ = 59 flowers per plot, SD = 66).
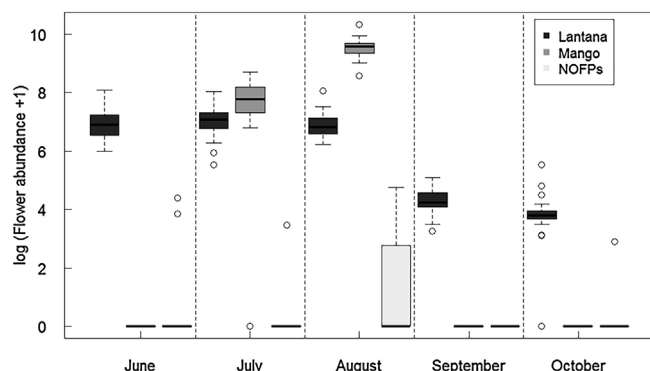
Fig. 2. The log (flower abundance + 1) of mango, *Lantana camara* and naturally occurring flowering plants (NOFPs) observed in all plots during June till October 2013. Mango supplies an abundance of flowers in July and August; whilst *Lantana* provides flowers throughout the season under consideration, the dry season. Given that it is the dry season, nofps in our plots had relatively few flowers during this study.

3.1. Lantana's effect on mango flower visitors

A total of 1468 insect-mango interactions were observed to over 1 325 000 mango flowers (Figs. 2 and 3, Table A3). Mean mango flower abundance in plots with *Lantana* present in neighbouring vegetation was significantly greater (t = 3.5, p < 0.001) than where *Lantana* was absent (mango floral abundance in plots with *Lantana* present: $\bar{x}$ = 9453, SD = 6696; Mango floral abundance in plots with *Lantana* absent: $\bar{x}$ = 6413, SD = 5694). We corrected for this by including mango flower density as an explanatory variable in the models. Mango flower visitation increased with mango flower density, and at lower mango flower densities, was significantly greater in plots where *Lantana* was present in neighbouring vegetation (Fig. 4, Table 1). Furthermore, the abundance of flower visitors increased with the presence of naturally occurring flowering plants (Table 1). Conversely, *Lantana* was associated with greater species richness of mango flower visitors at high mango flower abundance (Table 1). The effect of naturally occurring flowering plants (NOFPs) was not significant (Table 1).

When insect groups were considered separately, *Lantana* had the same quantitative interactive effect with number of mango flowers on visitation to mango for flies and butterflies, but not for bees, ants or

beetles (see model results in Table A4, online Appendix). For bees, the number of visits to mango flowers increased with both the number of flowers and presence of *Lantana,* but there was no interactive effect for beetles and ants, visitation to mango flowers did not vary with mango flower abundance, nor the presence of *Lantana.*

3.2. Support of mango flower visitors by Lantana

During mango flowering, visitation to *Lantana* flowers increased by 92% in comparison with the period before, decreasing again by 89% after mango flowering. Of the 75 species visiting mango, 27% visited *Lantana* before, 48% during and 40% after mango flowering. The abundance of visits was much lower, however, with 18%, 19% and 16% of all flower visits to *Lantana* before, during and after mango flowering by species that had visited mango. When number of visits per flower by the 90 species that visited mango was compared between mango, *Lantana* and naturally occurring flowering plants, summed over all three seasons, there was no significant difference in visits per flower to mango and *Lantana*, however, the number of visits per flower to nofps was significantly greater than to mango and *Lantana* flowers (R^2 = 0.04, F = 4.1, dof = 2 and 219, p = 0.018; online Appendix Fig. A1).

The importance of *Lantana* in the diet of mango flower visitors also varied with timing of mango flowering, whether or not honey bees were included in the dataset. When honey bees were included in the dataset, during mango flowering, Muller's index for *Lantana's* effect on mango flower visitors was 0.48 ± 0.07. This was significantly greater than before (0.03 ± 0.02; p < 0.001) or after (0.32 ± 0.07; p < 0.05) mango flowering. When honey bees were excluded, *Lantana*'s effect on mango was still significantly lower before (0.07 ± 0.06; p < 0.05), and after (0.12 ± 0.06; p < 0.001) than during (0.31 ± 0.06) mango flowering (online Appendix Fig. A2).

For species that visited both *Lantana* and mango, the frequency of visitation by groups of species to the crop and the invasive were very different over the entire time period. For example, during mango flowering, beetles visited mango almost 12 times more often than they visited *Lantana,* whereas butterflies were seen 12 times more frequently on *Lantana* than mango. Overall, during mango flowering, bee species were seen almost 4.5 times more often on mango than *Lantana* during mango flowering (see Table 2, and online Appendix Table A5). Given
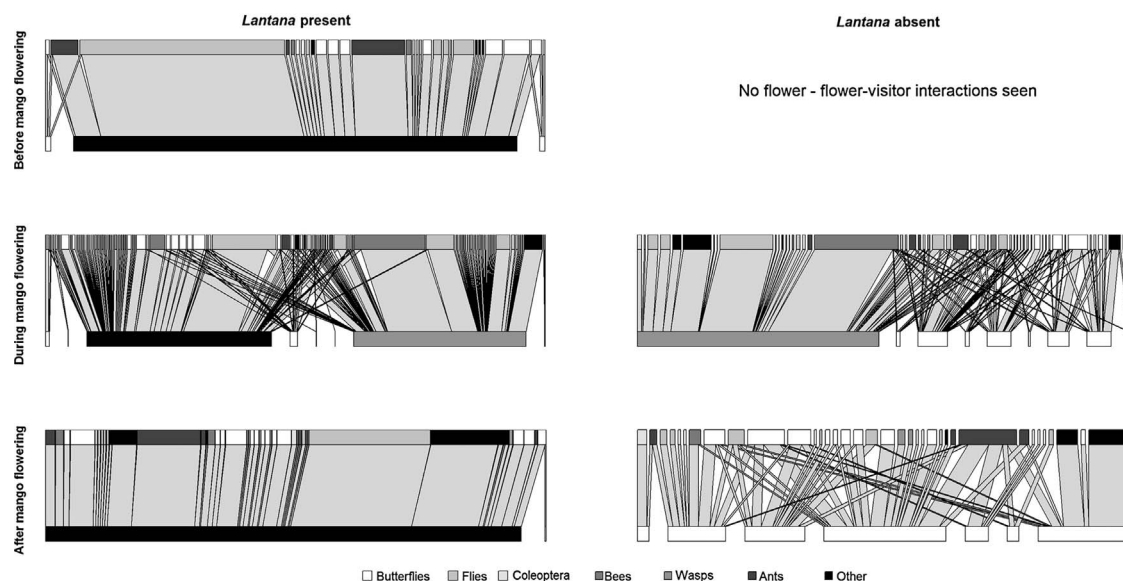

Fig. 3. Flower-visitation webs where *Lantana* is present and absent in nearby natural vegetation, before, during and after during mango flowering. These webs represent data pooled for all plots. Each plant and insect species is represented by a rectangle (full species list provided in Table A3, online Appendices). Rectangle width represents overall species abundance and the size of the interaction lines represent number of insects visiting each plant species. The top row of the networks indicates plant visitors, the bottom row, plant species. In the bottom row, *Lantana* is indicated in black, mango in grey and all other naturally-occurring flowers, in white.
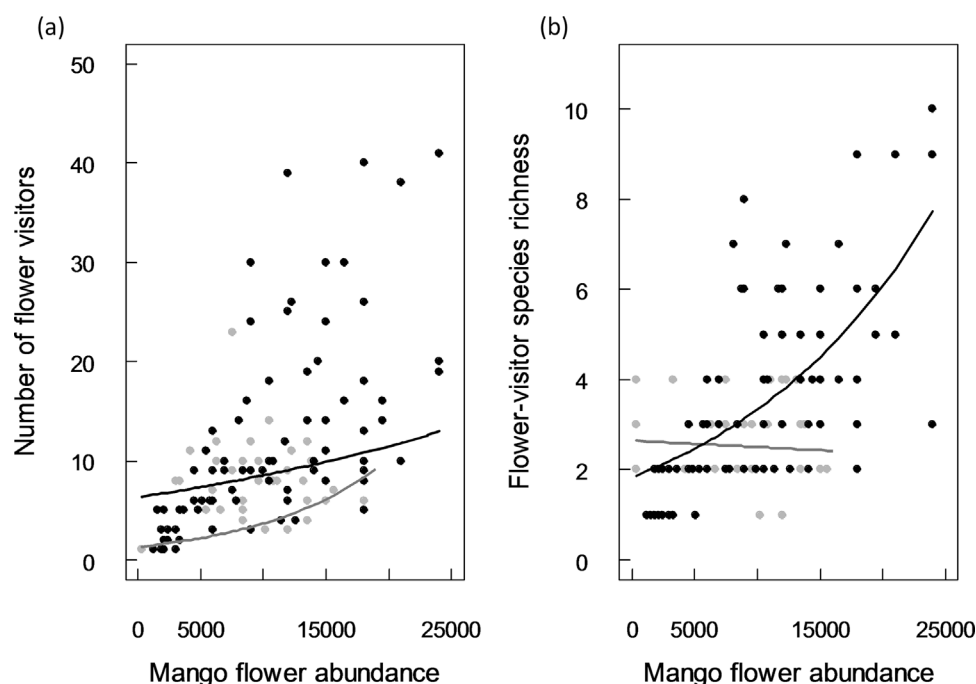
Fig. 4. Overall mango flower visitation by number of visits (a) and species richness (b) for all mango plots adjacent to natural vegetation with *Lantana* present (black line) and absent (grey line), during July–August 2013.

Table 1
The effect of floral abundances of mango (Mango fl.abnd), *Lantana* (*Lant* fl.abnd) and NOFPs (other naturally occurring flowering plants; NOFP.fl.abnd), the presence/absence of *Lantana* and interactive effects between these on mango flower visitation and species richness. The best model was that with the lowest AICc. Likelihood ratio tests calculated P-values during stepwise elimination, where models were compared for significance. 'ns', non-significant = $P > 0.05$. '–', variable not included in the model. Variance explained for flower visitation was 47.5% for fixed effects, and 62.2% for fixed and random effects. For species richness, fixed effects explained 21.1% of the variance, and fixed and random effects explained 32.2% of the variance.

Variables included in model	Model 1 (best model)	Model 2	Model 3	Null model
Number of flower visits to mango (Poisson error distribution)				
Mango fl.abnd. (F_1)	< 0.001	< 0.001	< 0.001	–
Lantana pres (F_2)	< 0.001	n.s.	< 0.001	–
Mango fl.abnd.: *Lantana* pres ($F_1 F_2$)	< 0.01	< 0.01	< 0.01	–
Log(*Lant*. fl.abnd. +1) (F_3)	–	n.s.	–	–
Log(NOFP.fl. abnd +1) (F_4)	< 0.01	< 0.01	–	–
Df	10	11	9	6
AICc	793.1	795.6	799.1	881.9
BIC	820.8	825.6	824.1	898.9
Best model: Without *Lantana*: $y = e^{1.1 + 0.63F1 + 0.1F4}$; With *Lantana*: $y = e^{2.0 + 0.29F1}$				
Flower visitor species richness (Poisson error distribution)				
Mango fl.abnd. (F_1)	n.s.	n.s.	n.s.	–
Lantana pres (F_2)	n.s.	n.s.	n.s.	–
Mango fl.abnd.: *Lantana* pres ($F_1 F_2$)	< 0.001	< 0.001	< 0.001	–
Log(*Lant*. fl.abnd. +1) (F_3)	–	–	n.s.	–
Log(NOFP.fl. abnd +1) (F_4)	0.051	–	0.051	–
Df	10	9	11	6
AICc	500.9	502.3	502.6	529.7
BIC	528.6	527.4	532	546.7
Best model: Without *Lantana*: $y = e^{0.86 - 0.03F1 + 0.06F4}$; With *Lantana*: $y = e^{1.1 + 0.38F1 + 0.06F4}$				
Second best model: Without *Lantana*: $y = e^{1.08 - 0.02F1}$; With *Lantana*: $y = e^{1.12 + 0.43F1}$				

Table 2
Number of visits to *Lantana camara* flowers by the most common shared insect flower visitors with mango in three different months, before with mango before (June), during mango peak flowering (August) and after (October) mango flowering in natural vegetation bordering mango orchards. Information of the contribution that each visitor species makes to the overall visitation of mango is also provided.

Flower Visitors Group	Species	*Lantana* flower interactions			Proportion of mango visits
		Before	During	After	
Diptera					
	Musca sp. 2	119	314	105	< 1%
	Musca sp. 3	5	20	3	< 5%
	Syrphidae sp.[a]	0	8	0	19.8%
	Tachinidae sp.	1	15	2	< 1%
Formicidae					
	Camponotus sp.	0	6	2	< 2%
	Pheidole sp.	15	2	8	< 2%
	Lepisiota sp.	31	36	55	< 2%
Apidae					
	Xylocopa caffra	2	81	6	< 1%
	Apis mellifera[a]	3	36	7	40.1%
Apocrita					
	Vespidae sp.	0	15	3	< 1%

[a] Known (i.e., based on previous research and the literature) mango pollinating flower visitors making-up at least 10% of total mango flower visitation.

that beetles were selecting mango in preference to *Lantana*. Honey bees were seen most frequently on mango during the peak of mango flowering, with over 500 visits by honey bees to mango flowers, and three and seven visits to *Lantana*, before and after mango flowering, respectively. Similarly, the beetle species seen most often on mango flowers were not seen on *Lantana* before or after mango flowering. Flies also showed this pattern, with the syrphid fly (*Ischiodon* sp.), the most commonly-observed fly on mango (248 visits), only seen making occasional (eight) visits to *Lantana* during mango flowering, and not at all when mango was not in flower.

3.3. Influence of Lantana on mango fruit production

Our production data set did not show evidence of spatial

that mango flowers were 7.6 times more abundant than *Lantana* flowers during mango flowering season, these trends suggest that butterflies were preferentially choosing *Lantana* over mango flowers, and perhaps
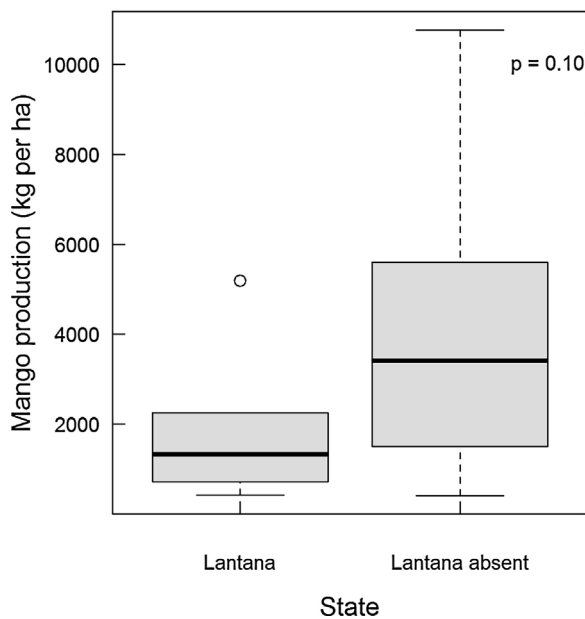
Fig. 5. Mango production for blocks on Bavaria mango farm, as a function of the presence or absence of *Lantana* in the neighbouring vegetation.

autocorrelation (p = 0.07). Neither mango flower abundance (p = 0.69) nor the presence of *Lantana* in bordering vegetation (p = 0.10, n = 20) had a significant effect on mango fruit production (mean ± s.d. = 9.4 ± 7.8 × 10^3 kg ha^{-1}), although there was a weak trend towards higher fruit production from mango orchard blocks neighbouring vegetation from which *Lantana* was absent (Fig. 5).

4. Discussion

Several studies have demonstrated an influence (i.e., positive, negative or neutral effects) of alien invasive plants on flower visitation of co-flowering plants in natural habitats, which in turn affects the native species' reproductive success (Bjerknes et al., 2007; Carvalheiro et al., 2008). To the best of our knowledge, this is the first study to examine the influence of an alien invasive plant on the flower visitation of a nearby flowering crop. In addition, because this study considered flower visitors before, during and after crop flowering, it enabled evaluation of the importance of the invasive as an alternative food source for the crop's flower visitors. We found that although the presence of *Lantana* was associated with increased mango flower visitor abundance and species richness in neighbouring mango trees, the invasive did not support mango flower visitors outside of mango flowering season, nor was it associated with increased mango fruit production at the field scale.

4.1. Lantana's effect on mango flower visitors

Although mango flower visitor abundance was positively correlated with that of mango flowers, *Lantana* was associated with greater abundance of mango flower visitors when mango flower density was low (Fig. 4), but not when it was high. At low mango flower densities, *Lantana* may have attracted more flower visitors to the vicinity, through a magnet effect (Thomson, 1978), thus facilitating visitation to mango. Where mango flower densities were high, however, the presence of *Lantana* was not associated with more visits to mango flowers (Fig. 4). This might be because at a certain density of mango flowers, the relative importance of mango and *Lantana* in attracting flower visitors through a floral display switches. Flower visitors are now attracted to the mango flowers themselves, which are now at densities sufficient to create a display; on arrival, the visitors are then distracted by the

nearby *Lantana,* and the role of *Lantana* changes from one of facilitation to one of competition. Furthermore, the abundance of flower visitors to mango increased with the abundance of NOFPs, a finding consistent with previous work that found that the presence of native flowers increased flower visitation to mango flowers, and fruit set (Carvalheiro et al., 2012). Interestingly, number of *Lantana* flowers added no extra explanatory power to the model, although number of naturally occurring flowers of other species did. This could be because almost without exception, when *Lantana* is present, its flowers are highly abundant (between 250 and 2000 flowers per sampled plot, mean = 1031). Naturally occurring flowers, however, varied considerably in their abundance (1–418 flowers, mean = 59, when present). Thus the effect of an increase in NOFP flower abundance would have been more discernible than increases in *Lantana* flower abundance, because the high abundance of *Lantana* flowers may have made the effect of additional flowers in attracting pollinators unimportant.

Lantana was associated with a greater number of species visiting mango compared to where *Lantana* was absent. This might be related to the fact that *Lantana* flower abundance and mango flower abundance were correlated, so there was an even more marked flower display where the two species were found together, and this may have attracted more species. In addition, *Lantana* has a longer flowering period than mango, and so *Lantana* may be important in supporting rarer species in the landscape when mango is not in flower.

Lantana may lure insects from the wider surrounding area to visit the less-obvious co-flowering crop flowers (Duffy and Stout, 2011; Johnson et al., 2003; Moeller, 2004), as it forms a large part of a collective floral display with mango when little else is flowering (Feldman et al., 2004; Rathcke, 1983). That *Lantana* is non-native is irrelevant for pollinators, so any attractive flower resource would have a similar effect (e.g. the native *Aloe greatheadii*, Carvalheiro et al., 2012). Planting indigenous species for this role might need to be encouraged with some payment system at first, until the benefits are demonstrated to landowners (Brown et al., 2016; Holzschuh et al., 2007).

Visitation rates to mango in this study may seem low (one visit per 900 mango flowers per 10-min observation period) but these visitation rates are consistent with those seen previously at this study site (e.g., Carvalheiro et al., 2010). Given that mango flowers in the dry winter season, when few insects and floral resources are available, such low rates are hardly surprising. Despite these low visitation rates, differences in fruit set have been observed in this system as a function of flower visitor abundance and species richness (Carvalheiro et al., 2012, 2010), so the low visitation rates do not indicate insufficient sampling.

Floral density of mango and presence of *Lantana* (fixed factors in the models) explained nearly 48% of the variance in the number of visits to mango flowers, but only 21% of the variance in flower visitor species richness. When random effects (month, plot and farm and cultivar) were considered, however, the variance explained for changes in abundance and species richness increased to 62% and 32%, respectively, highlighting the influence of timing, geographical location and cultivar. Variation explained by geographical location captures variation associated with floral diet preferences, floral species availability, variation in floral attractiveness of various plants, availability of nesting sites as a function of soils and disturbance as well as environmental variation (in temperature, humidity and precipitation). Other elements contributing to unexplained variation for both mango flower visitation and species richness may include density-linked factors (i.e., the presence of co-occurring plants at a larger scale that are also important to pollinators), and perhaps varying attractiveness of mango cultivars to flower visitors.

4.2. Support of mango flower visitors by Lantana

Despite the presence of *Lantana* being associated with an increase in mango flower visitation, flower visitor species shared by mango and *Lantana* differed in their frequency of visits to the two species. *Lantana*

may have acted as a magnet, attracting flower visitors to the vicinity, and on arrival, some species may then have switched to visiting mango, or *vice-versa*.

Plant species that are visited by mango flower visitors before or after mango flowering can be considered to facilitate mango, but species visited by mango flower visitors during mango flowering may be either facilitators or competitors, if they divert pollinator attention or if mango pollen is deposited on their flowers instead of on other mango flowers. The importance of *Lantana* to mango-visiting species was low before and after mango flowering, and greatest when mango was in flower. This was the case whether or not *Apis mellifera* was included in calculation of indirect effects (to account for the addition of managed honey bees during mango flowering). Complete exclusion of *A. mellifera* from the dataset is not completely accurate, as *A. mellifera* is also an indigenous, wild pollinator in our study area. Nevertheless, the importance of *Lantana* to mango pollinators was significantly lower before and after mango flowering whether or not honey bees were included, suggesting that *Lantana* is not important for both managed and wild mango flower visitors when mango is not flowering. Before mango flowering, Müller's index was ~ one tenth of that after mango flowering, when honey bees were included in the analysis. When honey bees were excluded, the importance of *Lantana* for mango pollinators before mango flowering was roughly half of what it was after flowering, and one fifth of what it was during mango flowering. Ideally, species that support crop flower visitors should do so before the crop begins to flower, allowing a build-up of potential pollinators, in time for crop flowering. Alternative forage out of crop flowering season is vital for the majority of crop pollinators, which have foraging periods much longer than the crop's flowering period (Simba, 2015). *Lantana* should be an important resource for mango flower visitors, as it flowers when little else is flowering in the surrounding vegetation, yet differences in frequency of visits to the two species and the low Müller's indices before mango flowering suggest that this is not the case.

We can discount the possibility that decline in visitation to *Lantana* before and after mango flowering is due to normal cyclical changes in insect populations, because visitation to *Lantana* was highest in the middle of the dry winter season (when mango is flowering), which would be an unlikely time for peaks in insect populations. It therefore appears that *Lantana* is far less useful than native plants like *Aloe greatheadii* (Transvaalalwyn) and *Barleria obtusa* (Bush violet), which have been found to support mango pollinators before mango flowering, and were associated with increased mango production (Carvalheiro et al., 2012).

4.3. Influence of Lantana on mango fruit production

Despite higher visitation to mango flowers in the presence of *Lantana,* our analysis of fruit production suggests that fields bordering natural vegetation with *Lantana* present have no greater fruit set than those without *Lantana.* These findings are slightly surprising, given that *Lantana* was associated with greater species richness of flower visitors. Species richness of flower visitors is often linked to better crop yield and quality (Bartomeus et al., 2014; Garratt et al., 2014; Hoehn et al., 2008), possibly because of niche complementarity (Hoehn et al., 2008) or behavioural interactions between pollinators (e.g., Brosi and Briggs, 2013; Carvalheiro et al., 2011) which enhance pollinator effectiveness. This line of evidence would suggest a facilitative role for *Lantana,* if it contributed to increased mango yield by increasing pollinator species richness at high mango flower densities. Our analysis of production data suggest this is not the case, however. The presence of *Lantana* may even reduce mango fruit set, given that there was a tendency for greater fruit set in the absence of this invasive species, but a larger dataset from more sites is needed to confirm this.

The lack of an effect of *Lantana* on mango fruit set may be partially explained by the fact that any effect of *Lantana* on fruit set and flower visitation is likely to decline with distance from the bordering vegetation in which *Lantana* is found. We investigated flower visitation to mango near the field margin only, but our production data was measured at the much larger scale of the field block. Previous work in the mango orchards in this system found declines in flying flower visitor abundance and species richness of about 20% of their maximum at distances of 500 m from natural vegetation (Carvalheiro et al., 2010). These declines were even steeper than those found in other studies, where flower visitor abundance declined to about half at just under 600 m from natural vegetation (Ricketts et al., 2008). In our study system, mango fruit production also declined with distance from natural vegetation: to about 60% of that found close to natural vegetation (Carvalheiro et al., 2010). Additionally, fruit abortion owing to heterospecific pollen deposition in mango flowers could even be higher when the source pollen is *Lantana*, but more detailed experiments on fruit set and pollen deposition would be needed to confirm this. It may also be that *Lantana* flower visitors are not effective mango pollinators, but further experiments investigating the effectiveness of different mango flower visitors would be necessary to resolve this.

Interestingly, there was greater variation in fruit production when *Lantana* was not present (Fig. 5). We speculate that this could be because *Lantana* seems to be associated with a greater abundance of flower visitors to mango when mango flower abundance is low, but not when mango flower density is high. Perhaps the presence of *Lantana* reduced variation in fruit set, owing to higher visitation when mango had fewer flowers. Finally, any economic benefit in terms of increased yield would need to be weighed against the management costs to control *Lantana*, and the cost of lost grazing in invaded adjacent natural vegetation (Vardien et al., 2012). *Lantana* could best be replaced by indigenous species like *Aloe greatheadii* and *Barleria obtusa* that support mango pollinators both during and outside of mango flowering season (Carvalheiro et al., 2012).

5. Concluding remarks

We offer the first study to investigate the effect of an invasive plant on flower visitation to a crop. We found that the invasive, *Lantana,* is associated with increased visitation by flower visitors to mango during mango flowering, although this effect was only important at low mango flower densities. *Lantana* was also associated with greater species richness of flower visitors to mango at high mango flower densities. Despite these positive effects during mango flowering, we found little evidence that *Lantana* supports mango flower visitors outside of mango flowering season. *Lantana* shares some flower visitors with mango but the relative abundance of these species differs. Furthermore, *Lantana* was particularly unimportant to mango flower visitors before mango flowering, when a good "supporting" plant should contribute to accumulation of flower visitors. Sharing of flower visitors with mango during mango flowering season may not necessarily imply facilitation, if pollen-dilution takes place, and this needs further investigation to determine whether successful pollination and increased fruit set are necessarily an outcome of greater visitor abundance associated with *Lantana*, because our analyses saw no improvement in production. Finally, the effect of presence of *Lantana* on mango may not extend far into the orchards (Albrecht et al., 2007; Carvalheiro et al., 2010), and the effect of distance (> 15 m) on flower visitation between *Lantana* and mango would also need to be assessed.

Findings of studies such as this are likely to vary with crop type, the traits of the invasive species, and crop flowering time. Mango flowers in the dry season, when little else is flowering, and *Lantana* is unusual in the area as it flowers (at least to some extent) throughout the year (Nel et al. unpublished data; Nimbalkar et al., 2011), potentially providing vital alternative resources to flower visitors. The importance of *Lantana* as a resource for pollinators would therefore have been expected to be high, but our analysis of indirect effects suggests that mango flower visitors make little use of *Lantana* outside of mango flowering season, and that *Lantana* is only important at low mango flower densities. Other

invasive species may have quite different interactions with crop pollinators. Crops that flower in the wet season may also have very different interactions with natural and invasive plant species in the surrounding environment. Future synthesis studies will likely be able to predict the traits of the crop and invasive that would indicate whether the invasive would be facilitative or competitive. Here, however, we found no facilitative effect.

Data accessibility

Data will be archived with Dryad Digital Repository.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.09.002.

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