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The edge effects of mango farming on flower visitor insect communities and epigeal ant species in North-Eastern South Africa.

By

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DECLARATION

I **LAVHELESANI DEMBE SIMBA**, hereby declare that the dissertation for the degree of Master of Zoology at the University of Venda for Science and Technology, hereby submitted by me, has not been previously submitted for a degree at this university or any other university, that it is my own work in design and execution and that all reference material contained therein has been duly acknowledged.

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Date 23/04/15

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ABSTRACT

The threat of a global pollination crisis to agricultural productivity has provided a motive for conservation within the context of ecosystem services while the use of predatory insects play a major role as biological control agents of insect pests. The link between biodiversity in natural vegetation and the provision of these ecosystem services was investigated in *Mangifera indica* (Mango) orchards using a network approach. Flower visitor sampling surveys were carried out for six months (June to October 2013 and January 2014) on three farms in plots (25 × 3 m) at varying distances (1 m, 10 m, 50 m, 100 m and 200 m) from the edge with natural vegetation, both into the mango orchard and into the natural vegetation. Epigeal ant communities were investigated using four pitfalls traps at each plot described above. Given that sampling was repeated at the three farms, for six months and in the same plots, generalized linear mixed models (GLMM) were used to assess the effect of distance, habitat and flower diversity on flower visitor and ant abundance and species richness. Flower visitor and epigeal ant species assemblage structure was analysed by the constrained redundancy analysis (RDA). Flower visitor networks were analysed to investigate plant pollinator interactions and how these interactions change with distance in the two habitats. There were more flowering plant species in the natural vegetation (NV) than in the mango orchard, however, there were significantly more flowers within mango orchards that included a combination of agricultural weeds and the mango flowers themselves. Abundance of wild flower resources on farms was positively correlated with mango flower visitation. Flying visitor species increased by 27% after the mango flowering season, but their abundance decreased by over 56%. Ant species richness, abundance and visitation rates increased after the mango flowering season. The abundance and species richness of flying flower visitors decreased with distance from the edge into the natural vegetation and the mango orchard. Flower visitor species composition in the orchard differed from that in the NV. Flower visitation networks in the mango orchards had higher linkage diversity in webs closer to the edge, suggesting that flower visitation tends to be higher in sites closer to the edge than those far from the edge. Epigeal ant abundance was highest in the edge habitat, decreasing into NV and the mango orchard. There were more ant species in the NV than in the mango orchard. The composition of ant assemblages differed significantly between NV and mango orchards. This study highlights how insect communities respond to edge habitats; flower visitation tends to be higher in sites closer to the edge than those far from the edge. Our results suggest that flower visitor diversity and network structure in the NV are more stable than flower

visitor webs in the mango orchards. There is higher stability in flower visitor network structure before mango flowering season than during and after mango flowering season. Plant diversity has a positive effect on flower visitors, maintaining native plant species within mango orchards may increase the diversity on mango flower visitors.

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explained by fixed effects only, and conditional R2 (R2c), measuring variation explained by both fixed and random effects, are given.

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CHAPTER 1: INTRODUCTION

Ecosystem services are the multitude of resources and processes that are supplied by ecosystems (grouped into provision, regulating, supporting and cultural categories) from which humans benefit (Millennium Ecosystem Assessment, 2005). The value of ecosystem services has been estimated by measuring their provisioning, determining their monetary value and designing tools for their management (Polasky, 2008).

Agriculture depends greatly on these services for pollination, nutrient cycling and control of crop pests, making it possible to measure the value of these services by estimating the change in the quantity and quality of agricultural production when the services have been removed or degraded (Power, 2010). Productivity of many major crops benefits from the presence of pollinator insects and pest control. A decline in the abundance of pollinators and the natural enemies of pests could therefore compromise global agricultural production.

1.1 Background information

One of the major reasons why ecosystem services have risen as a motive for conservation biology is the global pollination crisis threatening agricultural productivity because of a decline in the abundance of animal pollinators (Kremen and Ricketts, 2000). Agricultural crops vary in their need for pollinators, from those that are self-pollinating, to wind pollinated and those that rely heavily on animal pollination. However, in the last half-century there has been an increase in the fraction of agricultural crops that depend on animal pollination (Klein *et al*., 2007). The main concern now is that with global demand, the rapid increase of cultivation of these pollinator-dependent crops has the potential to trigger future pollination problems for both the agricultural crops and the native species surrounding them (Aizen and Harder, 2009).

About 65% of plant species require pollination by animals and analysis of data from 200 countries shows that 75% of crop species of global significance for food production rely primarily on insects (Klein et al., 2007). This dependence is higher in the developing world (Aizen *et al*., 2008), and the loss of insect pollinators could reduce total agricultural production by 3-8%, increasing the demand for agricultural land in the developing world, and contributing to global environment change (Aizen *et al*. 2009).

In South Africa, many farms make use of managed honeybees (*Apis mellifera*), but recent studies found that honeybees do not pollinate crops as efficiently as native pollinators (Russo *et al*. 2013; Greenleaf and Kremen 2006; Garibaldi *et al*. 2013). Based on mango production data from the Limpopo eastern low-veld farming area, Carvalheiro *et al*. (2010) found that the presence of managed hives did not improve fruit set significantly. However, distance from natural vegetation had a significant negative effect on mango production, highlighting the importance of natural vegetation as a source of mango pollinators (Carvalheiro *et al*. 2010). The maintenance of native pollinator and honeybee populations depend greatly on the diversity of flower resources (Kremen *et al*. 2004; Carvalheiro *et al*. 2012). Given that Carvalheiro *et al*. (2010) found that flower visitor species richness, abundance and pollination services all decline with distance from natural areas adjacent to *Mangifera indica* plantations, the question arises as to how flower visitor assemblages change in species composition, ecological network structure and complexity with distance from the edge between natural vegetation and orchards.

Most pests are injurious because of their biological characteristics, species abundance, high fecundity and rapid reproduction (Gherardi and Angiolini, 2004). The distribution and abundance of crop pest insects is directly dependent on environmental factors (Hoffmann and Frodsham, 1993), but are also often controlled by their natural enemies (Klemola *et al*. 2002). Ants are widely used in agroecosystems because ants they can affect pest control (Lobry de Bruyn, 1999). A previous study by Henri et al. (unpublished) found that tephritid fly pupae were preyed on by a generalist predatory ant species, *Pheidole megacephala*.

1.2 Research questions

1) Flower visitation

- How does flower diversity and abundance differ between the natural vegetation and mango orchards?
- How does flower visitor diversity (abundance, richness and composition) change over time and with distance from the edge into the mango orchards and the natural vegetation respectively?
- How does flower visitor web structure change over time and distance from the edge into the mango orchards and the natural vegetation respectively?

2) Ant distribution

- How do ant abundance, species richness and species composition change with distance from the edge into the orchards and the natural vegetation?
- Which ant species dominate the ant assemblages and how do their relative abundances change with distance from the edge?

1.3 Research aims and objectives

1.4.1 Aim

To determine the role of natural habitats as a source of flower visitors and pest's natural enemies (epigeal ants), in terms of species composition, and how that role changes over time and during the peak of mango flowering season

1.4.2 Objective

To use diversity and a network approach to quantify the benefits of natural ecosystems to adjacent agricultural systems as a source of beneficial insects, thus investigating the link between biodiversity and the provision of ecosystem services.

1.4 Null hypotheses

- There is no difference in the abundance, species richness and community composition of flower visitors in mango plantations and in the natural vegetation, nor does this change with distance from the edge of the two habitats.
- Ecological network structure and complexity do not vary visitors in mango plantations and in the natural vegetation, nor does this change with distance from the edge of the two habitats.
- There is no difference in the abundance, species richness and community composition of epigeal ants in mango plantations and in the natural vegetation, nor does this change with distance from the edge of the two habitats.

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

Mangifera indica is a tropical plant found in the order Spindales, family Anacardiaceae, that orginated from Southern Asia (DeCandolle, 1884; Kaur *et al*., 1980). It requires tropical climates at low altitudes and dry winter seasons for flowering and fruit set (Watson and Dallwitz, 1992). Mango flowers are born on terminal inflorescences that are broadly conical; the inflorescences bear hundreds of flowers. They have two forms of flowers occurring in the inflorescences, male and hermaphrodite (Bally, 2006).

Given that Carvalheiro *et al*. (2010) found that flower visitor species richness, abundance and pollination services all decline with distance from natural areas adjacent to *Mangifera indica* plantations, the question arises as to how flower visitor assemblages change in species composition and how the ecological network structure and complexity vary with distance from the edge between natural vegetation and orchards, into orchards and into natural vegetation.

The main pollinators of mango are wind and insects such as wasps, ants, flies and bees (Jiron and Hedstrom, 1985; Bally, 2006). Fajardo *et al*. (2008) studied the insect pollinators and floral visitors of mango looking at the efficiency of insect pollinators and flies in a farm. They found that out of 21 species of insects that visited the mango flowers, the primary pollinators were stingless bees, calliphorids, syrphids and honey bees. Blowflies, house flies and tachinid flies are considered to be better pollinators of mango flowers and although honey bees are preferred as pollinators by many farmers, their large bodies relative to the mango flowers affect their efficiency as pollinators (van den Berg, 2001).

2.2 The role of ants in Agro-ecosystems

Mangifera indica is attacked by a diverse group of insects including fruit flies such as *Ceratitis rosa*, *Ceratitis capitata* and *Ceratitis cosyra* (Bally, 2006). Predatory insects play a major role as biological control agents of insect pests (Smith *et al*., 1997), the most important biological control insects include ants Hymenoptera: Formicinae (Basedow and Bernal-Vega, 2001). Ants have been used for pest control for more than 1700 years (Holldobler and

Wilson, 1990). Ants' aggressive behaviors eliminate other insects and are also very important biological control agents of pest insects in mango (Krull *et al*., 2004).

Ants have a complex interaction with herbivores, pollinators and seed dispersers (Schemske and Horvitz, 1988), in ways that could be beneficial or detrimental to plants they live in or around (Holldobler and Wilson, 1990; Altshuler, 1999; Levey and Byrne, 1993; Willmer and Stone, 1997 and Yeo *et al*., 2011; Weilgoss *et al*., 2014). Aggressive ants act as plant guards to some plant species by protecting their leaves, flowers and fruits from other insects (Bentley, 1977; Altshuler, 1999; Gibb and Hochuli, 2003; Wielggoss *et al*., 2014). Ants reduce the population of some pest species at their larval stage (Smiley, 1986). However, Ants are well known to protect pest species such as mealybugs and scale through trophobiosis from parasitoids (Sharley *et al*., 2008).

Ant visitation to extra-floral nectaries may differ in the same habitat depending on the variety of nectar source and the ant species preference (Apple and Feener, 2001). The variation in ant visitation can also be explained by the interaction between ants and flying pollinator's competition for nectar (Ashman and King, 2005). Plant pollination by ants has been said to be rare (Holldobler and Wilson, 1990), but the interaction of ants and winged insects on plants can increase fruit set (Atshuler, 1999), and recent studies show that flower visiting ants can also be as effective as flying flower visitors in plant pollination (Gomez 2000; Ashman and King, 2005; Carvalheiro *et al*. 2010).

2.3 Landscape influences on agriculture

The landscape of an agro-ecosystem can greatly influence the delivery of ecosystem services. Agricultural landscapes vary from simple landscapes with one or two cropping systems, to complex mosaics of diverse cropping systems embedded in a natural habitat matrix (Power, 2010). The movement of organisms across the agricultural landscape is essential for pollination and biological control services, with pollinators and natural enemies moving among natural and semi natural habitats for refugia and resources that are scarce in the crop fields (Kremen *et al*. 2007).

Agricultural intensification leads to a decline in landscape complexity with a loss in semi-natural habitats, fragmentation and degradation, which may reduce biodiversity, affect web complexity, whilst changing the structure of the food web interactions and associated ecological processes (Thies and Tscharntke, 1999). Pollination by insects is highly affected by habitat fragmentation (Simonetti and Henryquez, 2006), especially those caused by human disturbances (Aizen and Feinsinger, 2003). These human disturbances can lead to the loss of foraging and breeding habitats for insect species (Fischer and Lindenmayer, 2007). According to ecological theory, an increase in vegetation diversity and structural complexity increases the diversity of insects with a chance of also affecting the surrounding habitats (Murdoch *et al*., 1972). Recent work by Gagic *et al*. (2011) in Germany failed to find a difference in richness of any trophic level across a landscape complexity gradient, however.

Landscapes have been altered and designed to improve diversity across agricultural lands, these management strategies include; the preservation and enhancement of remnant natural vegetation within and around crop fields (Cunningham *et al*., 2002), maintaining plant diversity by implementing appropriate mixed farming systems, rehabilitating degraded lands and reintroducing plants that are preferred by pollinators (Handini, 2013). Some studies show that pollinator richness and abundance can benefit greatly from the use of organic management (Holzschuc *et al*., 2008; Gabriel *et al*., 2010).

2.4 Ecological Networks

Food webs have been used in the past to investigate network topology, network stability and robustness in natural areas. They are useful in answering applied science questions, assess restoration of community structure, community functioning, and the resilience of restored communities to future species loss (Memmot, 2009). Pollinator functions and their importance can be determined by constructing visitation networks and pollen transport networks (Gibson *et al*., 2006) and ecological networks can capture the components of ecosystem services of pollinators in restoration to evaluate restoration success (Forup *et al*. 2008).

Food-web data have been used to suggest that maintaining diversity of flower resources within farmland can help maintain pollinator communities (Carvalheiro *et al*., 2011). Gibson *et al*. (2006) studied pollinators of rare plant species and found that rare species shared pollinators with other more common plant species in the community. These plant species may be primary food sources for the pollinators and essential for the continued survival of the rare species. This study will make use of ecological networks to study how plant-pollinator interactions change with distance and time in the mango orchards and the natural vegetation.

CHAPTER 3: METHODS

3.1 Study area and design

The study took place on three farms (Bavaria, Mohlatsi and Venden) located near Hoedspruit (Maruleng municipality) within the Kruger to Canyons Biosphere, Limpopo Province (24º24'58.44" S and 30º52'35.13" E, Fig. 1). The vegetation of the area is part of the savannah biome and is classified as Granite Lowveld with average temperature ranging from 3.7 ^{0}C in winter to 38 ^{0}C in summer (Mucina and Rutherford, 2006). Hoedspruit receives an annual rainfall of 410 mm, with average monthly rainfall ranging from 2 mm in winter and 189 mm in summer (Barrett *et al*., 2006). Bavaria and Venden are situated along the R527 road, east of Hoedspruit, 6.8 km away from each other, while Mohlatsi is 21.4 km south-east and 14.8 km south of Bavaria and Venden, respectively (Fig 2).

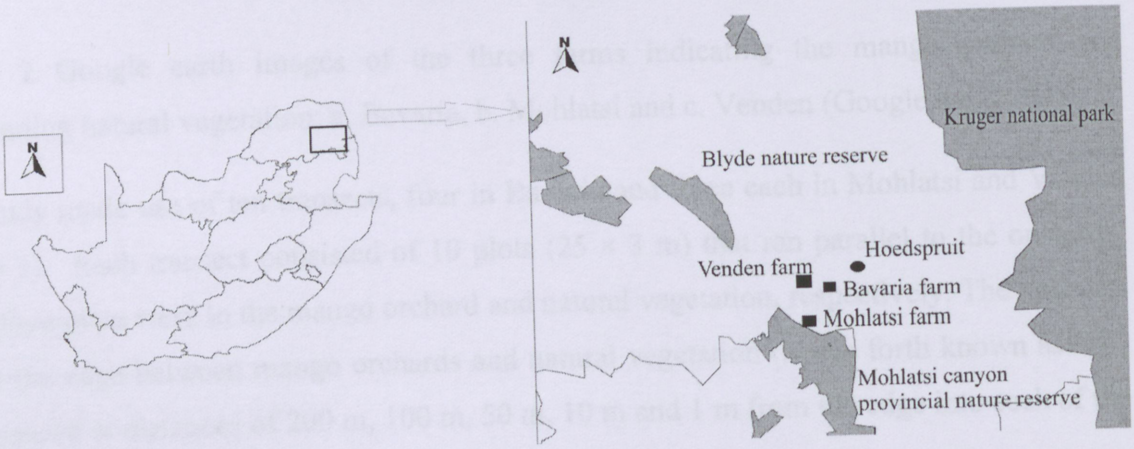


Figure 1 A map of South Africa highlighting the study area.

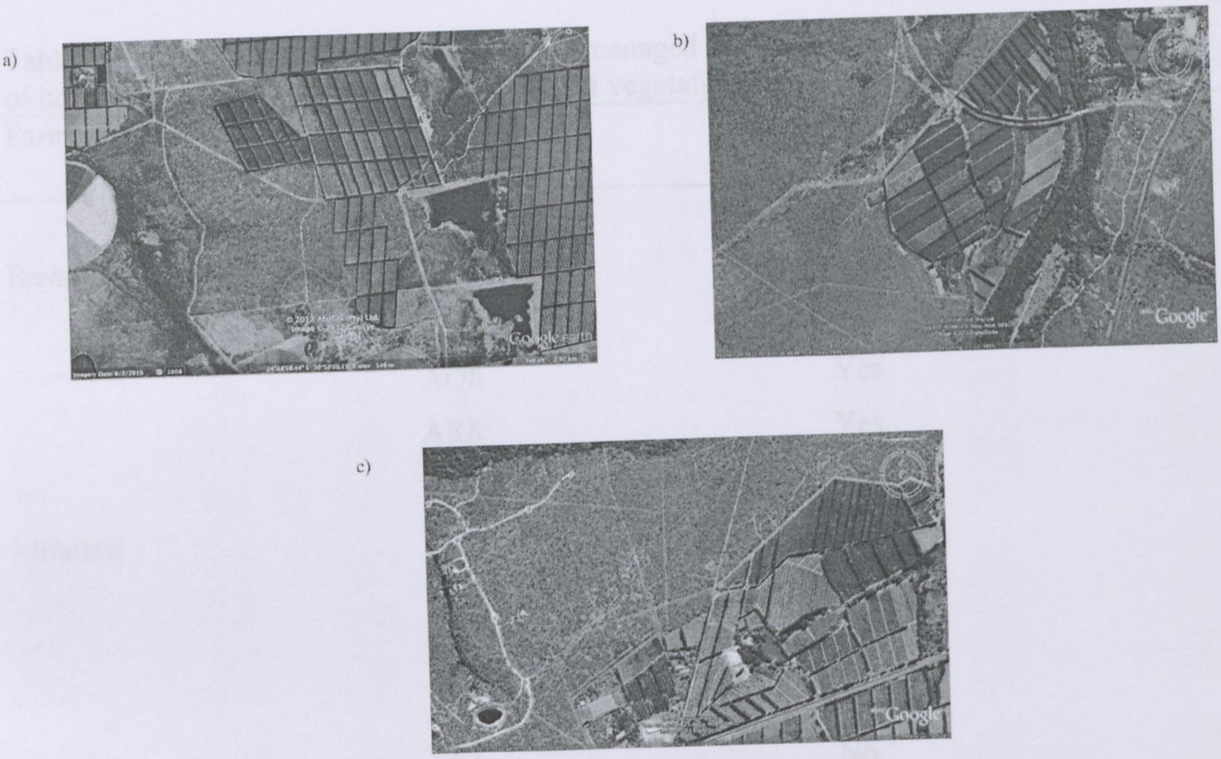


Figure 2 Google earth images of the three farms indicating the mango orchard and surrounding natural vegetation; a. Bavaria, b. Mohlatsi and c. Venden (Google inc, 2009).

The study made use of ten transects, four in Bavaria and three each in Mohlatsi and Venden (Table 1). Each transect consisted of 10 plots (25 × 3 m) that ran parallel to the orchards' edge. Five plots were in the mango orchard and natural vegetation, respectively. The transects across the edge between mango orchards and natural vegetation (hence forth known as NV) were spaced at distances of 200 m, 100 m, 50 m, 10 m and 1 m from the edge into each of the two habitat types (Fig. 3).

Table 1 Ten transects with and presence of managed bees. Naturally-occurring populations of honeybees are also found within the natural vegetation.

Farm	Transect	Managed bee hives present?
Bavaria	AM7	Yes
	AM8	Yes
	AQ8	Yes
	AR8	Yes
Mohlatsi	MTA1	Yes
	MTA2	Yes
	MTA3	Yes
Venden	VS1	No
	VTA	No
	VSU	No

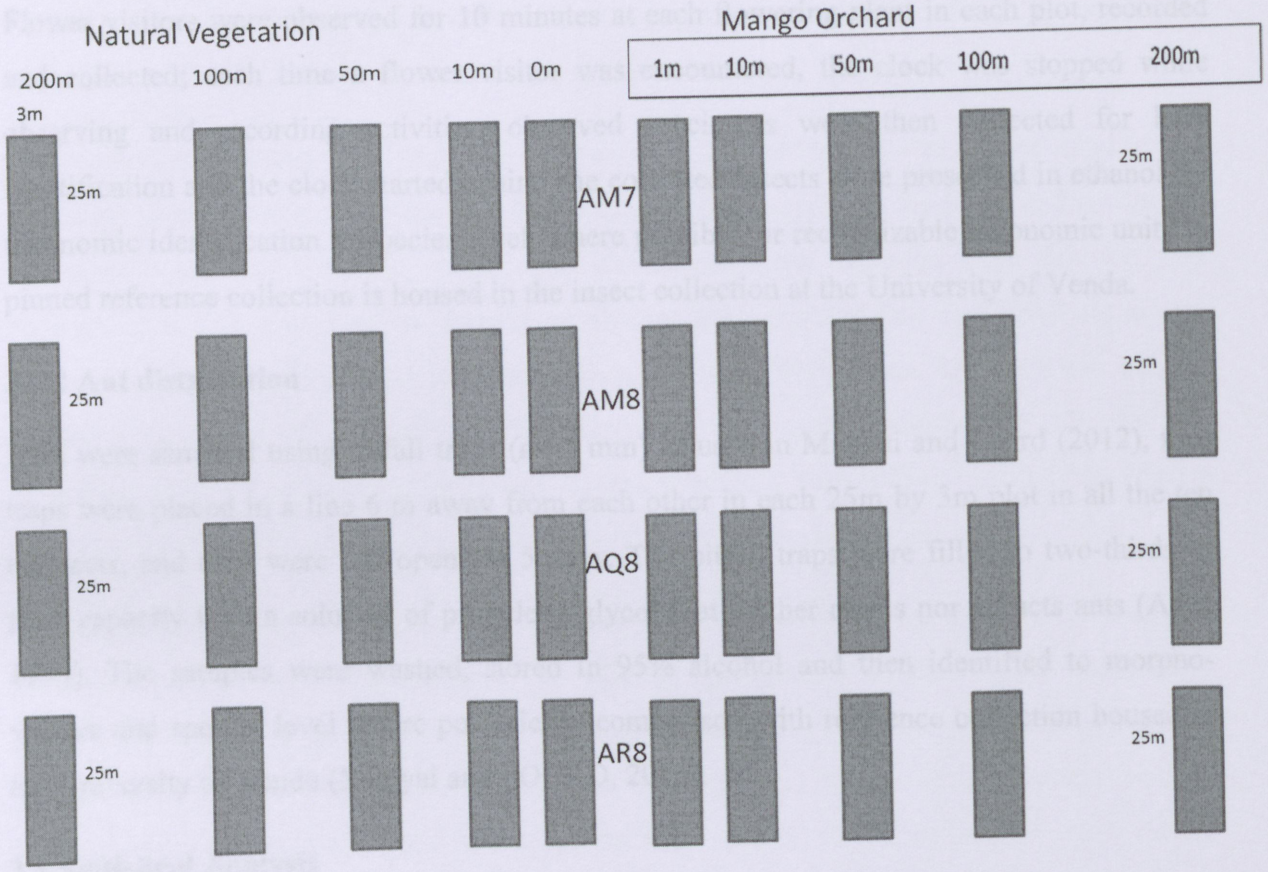


Figure 3 Bavaria study site design, showing the four transect AM7, AM8, AQ8 and AR8 with the different plots and distances from the edge in to the mango orchard and the NV.

3.2 Sampling

3.2.1 Flower visitation

Surveys were carried out once a month for six months between 08h00 and 15h00. *Mangifera indica* starts flowering in July, while flowering peaks in mid-August and ceases by the end of September. Sampling was done between June 2013 to October 2013, and once more in January 2014.

Every flowering plant observed was recorded, identified to species level, and the total number of flowers within plots counted. As *Mangifera indica* is a hyper-abundant flowering species, the total number of flowers was estimated by counting the number of open flowers of three randomly selected inflorescences (Carvalheiro *et al.*, 2010). The average was multiplied by the total number of inflorescences counted in the plot. This was done for all hyper-abundant flowering plants.

Flower visitors were observed for 10 minutes at each flowering plant in each plot, recorded and collected; each time a flower visitor was encountered, the clock was stopped while observing and recording activities, observed specimens were then collected for later identification and the clock started again. The collected insects were preserved in ethanol for taxonomic identification to species level, where possible, or recognizable taxonomic unit. A pinned reference collection is housed in the insect collection at the University of Venda.

3.2.2 Ant distribution

Ants were sampled using pitfall traps (ø 62 mm) as used in Munyai and Foord (2012), four traps were placed in a line 6 m away from each other in each 25m by 3m plot in all the ten transects, and they were left open for 5 days. The pitfall traps were filled to two-thirds of their capacity with a solution of propylene glycol that neither repels nor attracts ants (Adis, 1979). The samples were washed, stored in 95% alcohol and then identified to morpho-species and species level where possible by comparison with reference collection housed at the University of Venda (Munyai and FOORD, 2015).

3.3 Statistical Analysis

Wilcoxon rank sum tests were used to examine whether there was a difference in richness and abundance of flowering species between the two habitats. To assess the effect of distance and habitat on flower abundance and floral richness, generalized linear mixed models (GLMM) with a log-link function and Poisson error distribution were performed in the R (R core development team, 2013) using the package lme4 (Bates *et al*., 2014), with flower abundance and floral richness as dependent variables, distance from the edge and habitat as fixed variables, farm and month as random variables. The model with the lowest Akaike information criterion (AIC) was selected as the best model (Burnham and Anderson 2002). Marginal R^2 (R^2_m, due to fixed effects only) and conditional R^2 (R^2_c, due to fixed and random effects) were calculated for the best model to determine how much of the variation is explained by fixed and random effects respectively (Nakagawa and Schielzeth, 2013). Smoothed lines were fitted to scatterplots of response variables using generalized additive models (GAM) (Wood, 2006).

Flower visitors were divided into two categories, flying visitors and crawling visitors (ants). Flower visitor abundance data were standardized to visitation rates by dividing the number of flower visitors by the total number of flowers observed in each plot. GLMM with loglink functions and Poisson error distributions were used to determine how flower visitor abundance and species richness varied with distance and time.

Constrained redundancy analysis (RDA) was used to analyse flower visitor (flying and crawling) and epigeal ant assemblage structure using linear species response models. Species that contributed less than 1% to the total abundance were excluded from this analysis. Forward selection was used to identify environmental variables that explained significant amounts of variation in species richness. IndVal analysis (R package "labdsv") was used to identify species that are associated with different farms, distances and habitat (Dufrêne and Legendre, 1997). A significant IndVal of 70 was used as a threshold for identifying species that were both specific and had high fidelity for each of these categories.

All spatial and temporal dynamics of flower visitor networks were analysed with the bipartite package in R (Dormann et al. 2008). Quantitative flower visitor webs were constructed for distances 200m to 100m (far from the edge) and 10m to 0m (closer to the edge) in the veld, and 200m to 100m (far from the edge) and 10m to 0m (closer to the edge) in the mango orchard, and before, during and after mango flowering season, with flower visitors on top of the web and plants at the bottom of the web. Network level metrics such as connectance, nestedness, number of compartments and linkage diversity were calculated for each flower resources web structure.

CHAPTER 4: RESULTS

4.1 Flower visitation

4.1.1 Spatial dynamics of flower diversity along a gradient between mango orchards and natural vegetation

A total of 322032 flowers on 78 plant species were recorded over the six month period (appendix A) in both mango orchards and NV. NV had more flowering plant species (56) than mango orchards (39), although this difference was not significant ($W = 71$, $P < 0.086$). There were significantly more flowers observed in the mango orchards than in NV ($W = 197$, $P < 0.0002$, see Figs. 4 and 6).

The best model for flower abundance identified distance, habitat type and the interaction between distance and habitat as significant variables (Table 2). The interaction between distance and habitat was positive indicating an increase in flower abundance with distance from the NV into the mango orchard (Fig 5, Table 2). Fixed effects explained 40% of the variation in flower abundance and the random effects explain only 9% of the variation ($R^2_m = 0.401$, $R^2_c = 0.492$, Table 2). Distance and habitat had a significant effect on floral species richness, explaining only 8% of the variation ($R^2_m = 0.079$, $R^2_c = 0.188$, Fig 7, Table 2).

Table 2 GLMM with Poisson distribution error showing the effect of distance on flower abundance and floral species richness. The change in AICc (ΔAIC) between the best model and the next best and the worst model are also given. The worst model was modelled by random effects only (farm and month). Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random effects, are given.

Response	Model	AIC (Best model)	ΔAIC (second best)	ΔAIC (worst)	R^2_m	R^2_c
Flower abundance	~ distance*** + habitat*** + distance : habitat***	106267	7454	87753	0.401	0.492

Model equation: $Y = e^{9.787 - 0.259 \times D - 1.050 \times NV + 0.521 \times D:NV}$

Flower species richness	~ distance*** + habitat***	144.5	3.3	5.3	0.079	0.188
	Model equation: $Y = e^{1.2 - 0.001 \times D + 1.607 \times NV}$					

*, < 0.05; **, <0.01; ***, <0.001

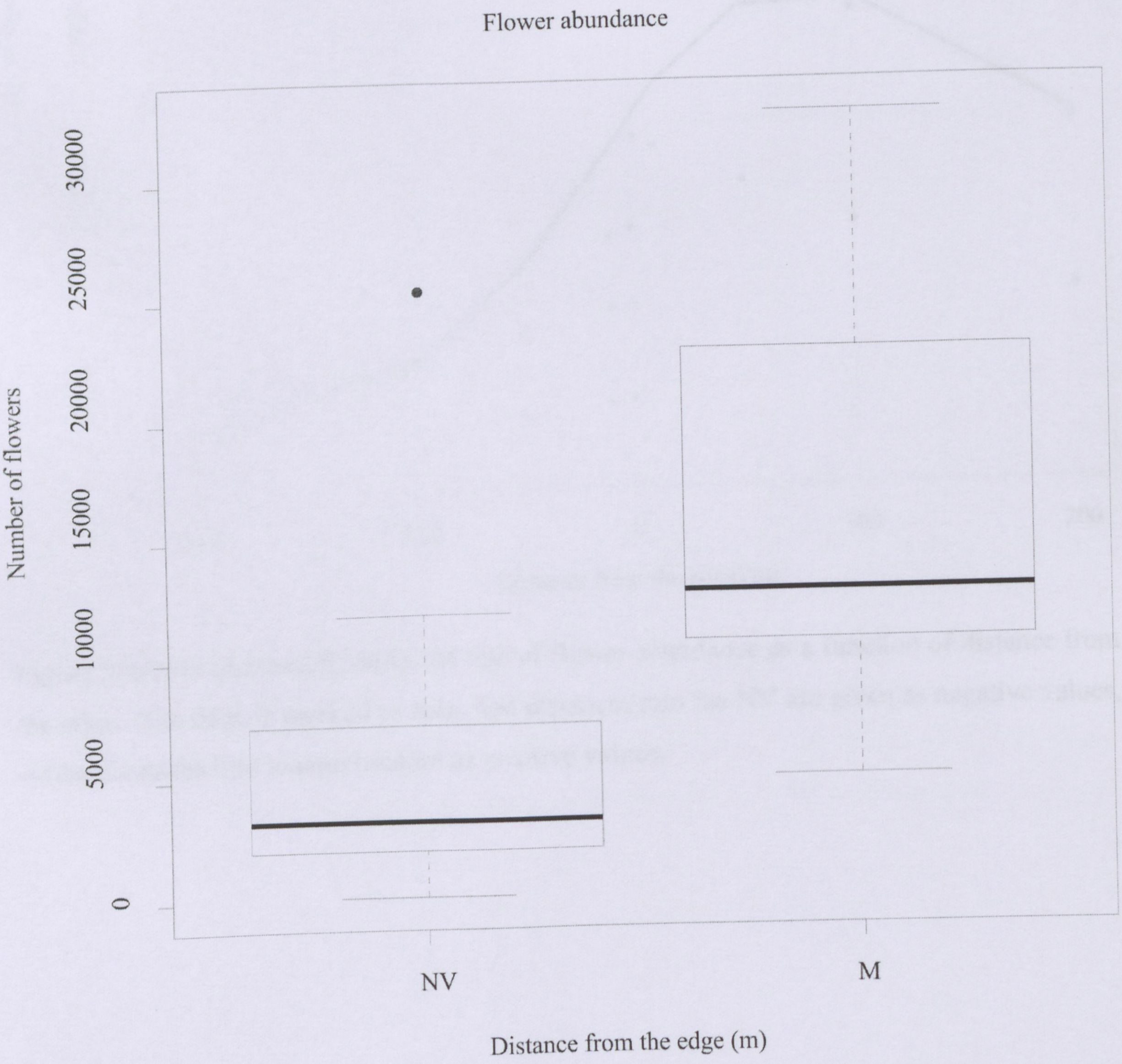


Figure 4 Boxplot of pooled flower data (i.e., over all months) in the mango orchard (M) and the NV (see Table 2 for statistical details). Boxplot represents the upper and lower quartiles, minimum and maximum values (i.e. 1.5 times the interquartile range), and the median. Outliers are shown as closed circles.

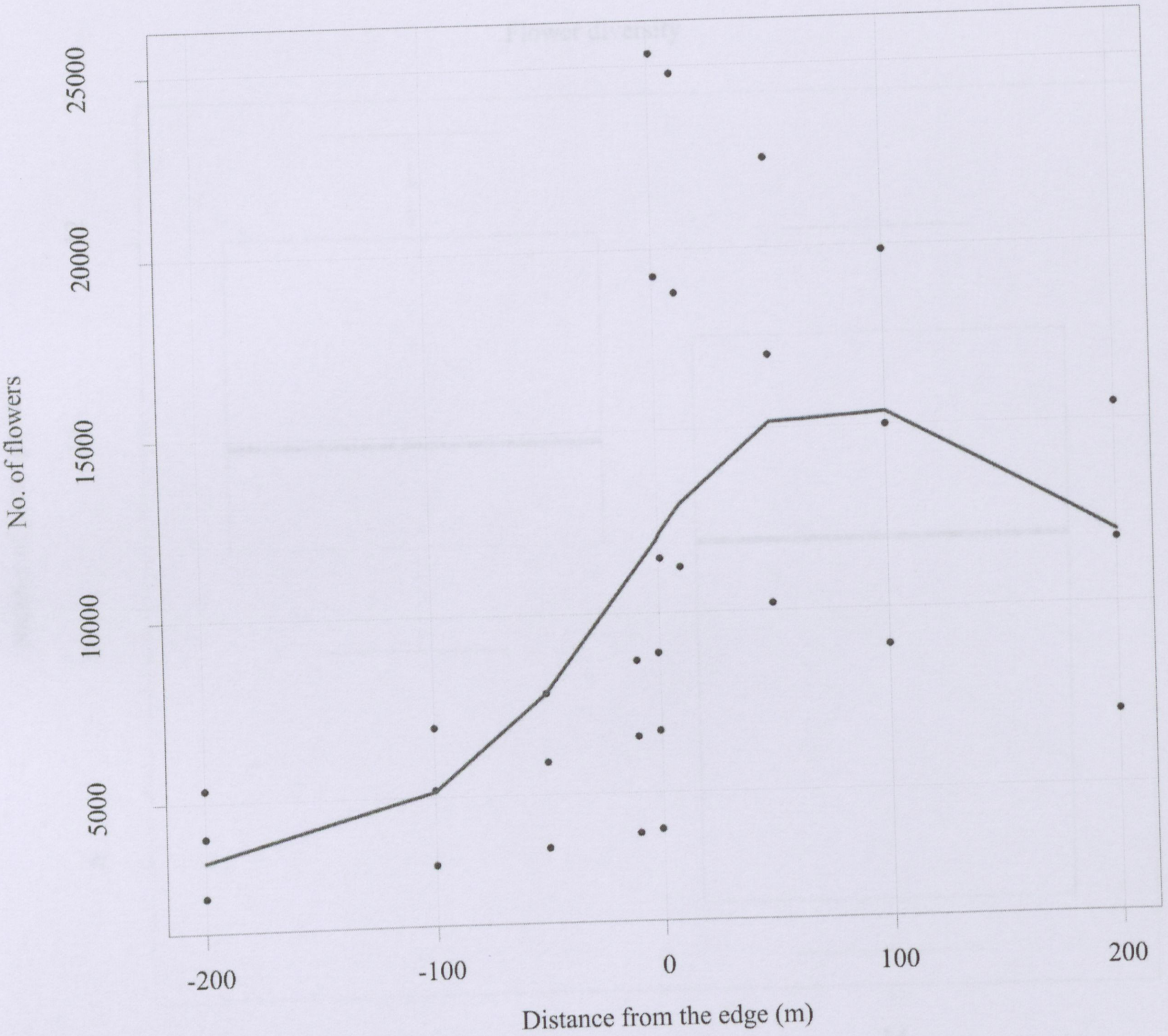


Figure 5 Scatter plot and fitted GAM line of flower abundance as a function of distance from the edge. The edge is marked as zero, and distances into the NV are given as negative values, whilst distances into mango orchard as positive values.

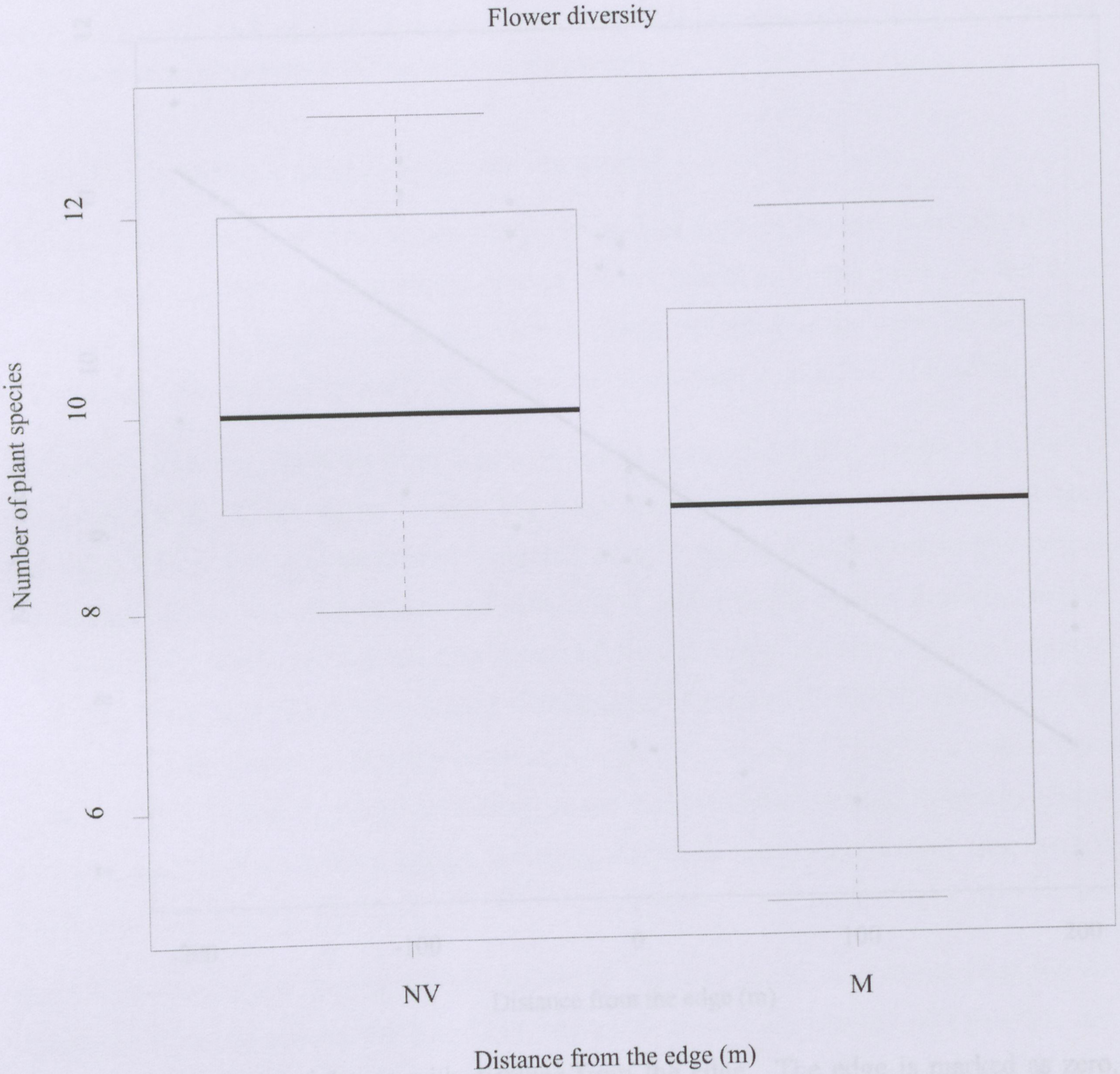


Figure 6 Boxplot of plant species richness in mango orchards (M) and the NV (V) of the three farms (see Table 2 for statistical details). Mango orchard, n = 39; NV, n = 56.

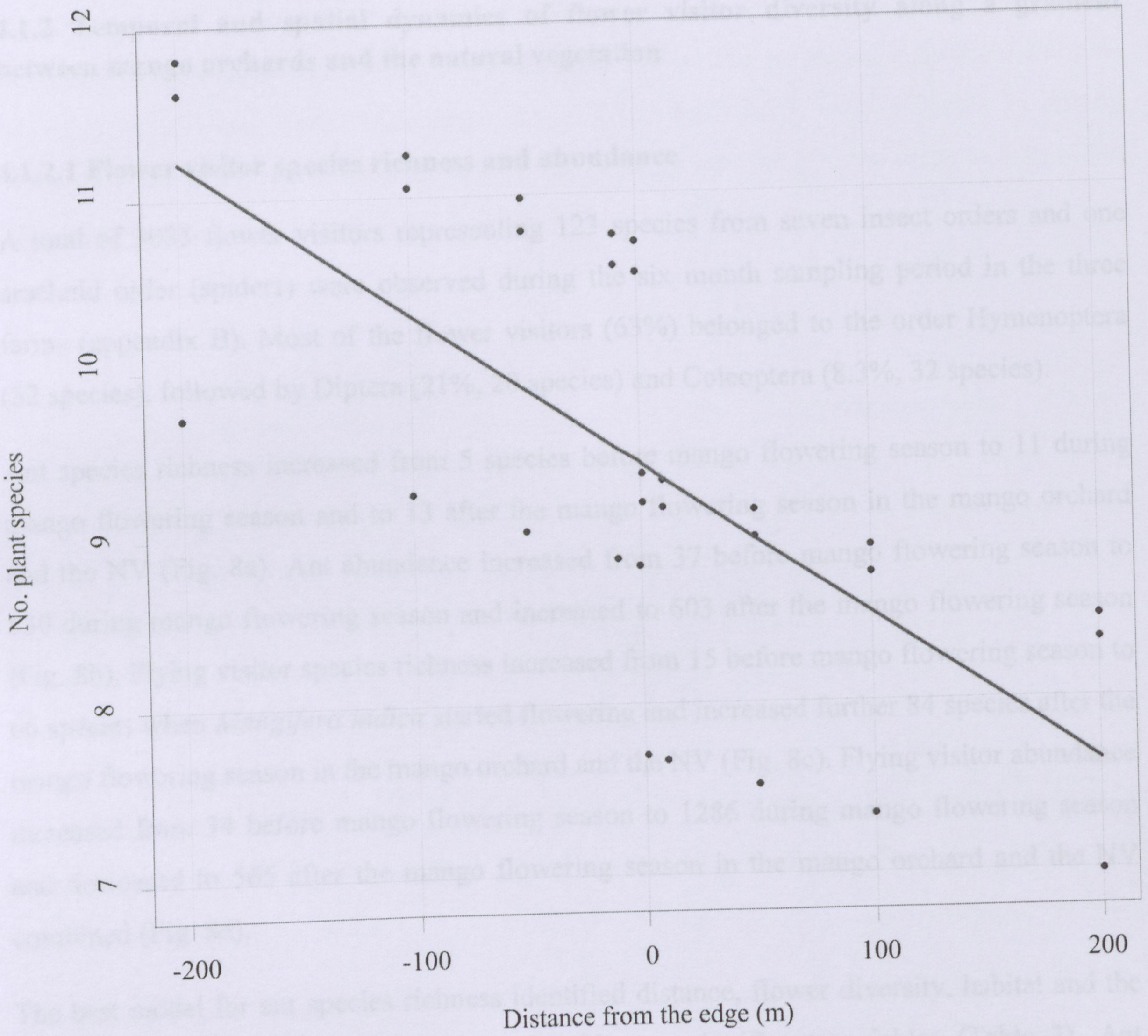


Figure 7 Plant species richness with distance from the edge. The edge is marked as zero, distances into NV are given as negative values, whilst distances into mango as positive values.

4.1.2 Temporal and spatial dynamics of flower visitor diversity along a gradient between mango orchards and the natural vegetation

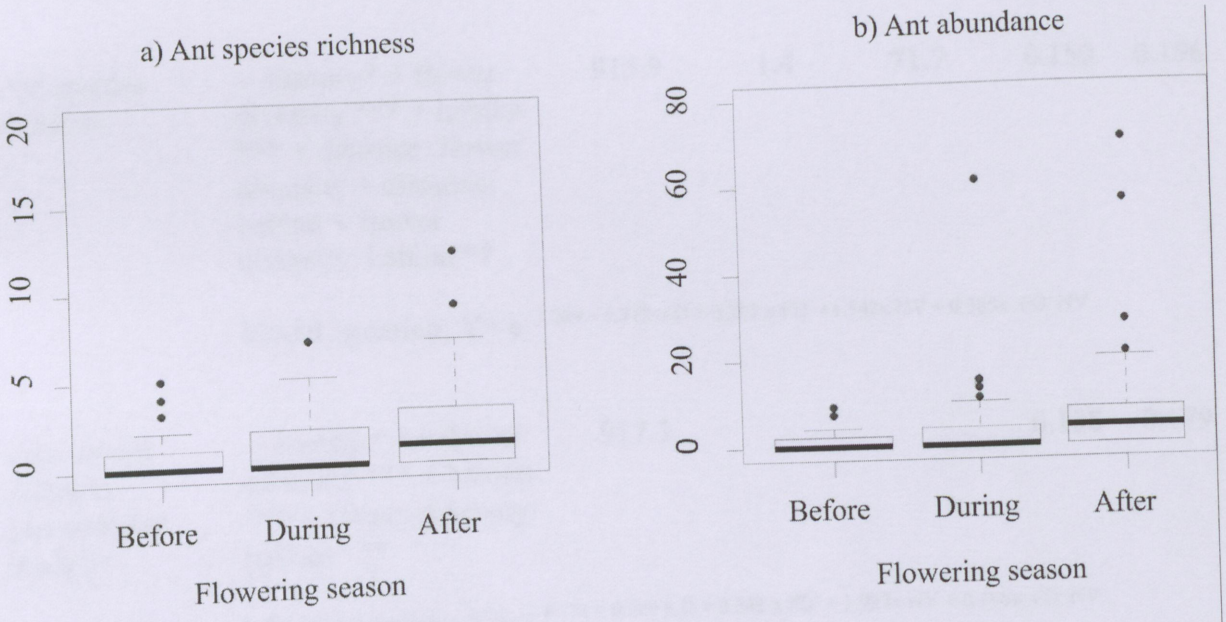
4.1.2.1 Flower visitor species richness and abundance

A total of 3085 flower visitors representing 123 species from seven insect orders and one arachnid order (spiders) were observed during the six month sampling period in the three farms (appendix B). Most of the flower visitors (63%) belonged to the order Hymenoptera (32 species), followed by Diptera (21%, 20 species) and Coleoptera (8.3%, 32 species).

Ant species richness increased from 5 species before mango flowering season to 11 during mango flowering season and to 13 after the mango flowering season in the mango orchard and the NV (Fig. 8a). Ant abundance increased from 37 before mango flowering season to 530 during mango flowering season and increased to 603 after the mango flowering season (Fig. 8b). Flying visitor species richness increased from 15 before mango flowering season to 66 species when *Mangifera indica* started flowering and increased further 84 species after the mango flowering season in the mango orchard and the NV (Fig. 8c). Flying visitor abundance increased from 34 before mango flowering season to 1286 during mango flowering season and decreased to 565 after the mango flowering season in the mango orchard and the NV combined (Fig. 8d).

The best model for ant species richness identified distance, flower diversity, habitat and the interaction between flower diversity and habitat as significant variables (Table 3). Ant species richness was highest in the NV and with high flower diversity, and decreased with distance from the NV into the mango orchard ($z = -6.403$ P, < 0.001, see Fig. 9a). Ant species richness was best explained by distance, flower diversity and the interaction between distance and habitat ($R^2_m = 0.158$, $R^2_c = 0.193$, Table 3). The fixed effects for ant abundance explained only 6% of the variation however ($R^2_m = 0.066$, $R^2_c = 0.066$). Ant abundance was greatest at the edge between NV and the mango orchards, decreasing with distance into both NV and mango orchards ($z = 3.48$, $P < 0.001$, Fig. 9b).

Flying visitor species richness was significantly influenced by distance, flower diversity, habitat and the interaction between distance and flower diversity explaining 23% of the variation ($R^2_m = 0.232$, $R^2_c = 0.374$). The number of flying visitor species also increased with distance from the edge into the NV but decreased from the edge into the mango orchard ($z = -7.535$, $P < 0.001$, Fig. 9c). Distance, habitat, flower diversity, the interaction between distance and habitat, the interaction between distance and flower diversity and the interaction between habitat and flower diversity were the fixed effects that explained significant amounts of variation in flying visitor abundance, $R^2_m = 0.186$ and $R^2_c = 0.193$ (Table 3). Flying visitor abundance increased with distance from the edge into the NV but decreased from the edge into the mango orchard ($z = -3.824$, $P < 0.001$, Fig. 9d).



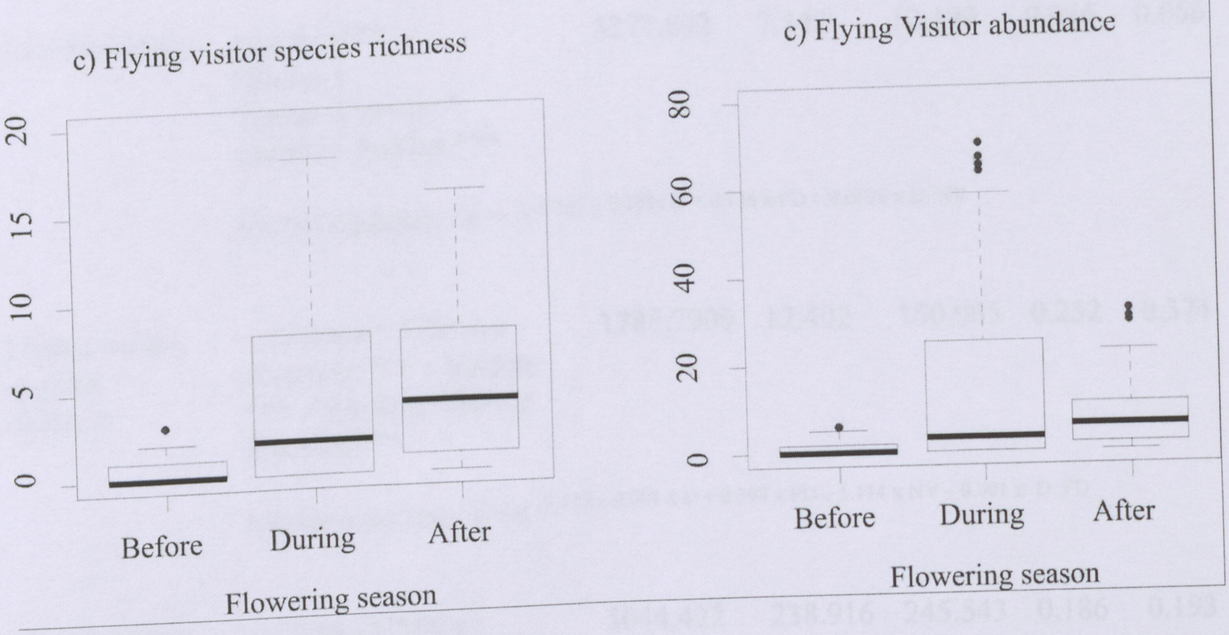


Figure 8 Boxplot showing ant and flying flower visitor abundance and species richness, before, during and after mango flowering season in the mango orchard and NV.

Table 3 The effect of Distance from the edge into mango orchard and into the NV on flower visitor abundance per flower and number of species. The change in AICc (ΔAIC) between the best model and the next best and worst are also given. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only and conditional R2 (R2c), measuring variation explained by both fixed and random effects, are given.

Response	Model	AIC	ΔAIC (best)	ΔAIC (worst)	R^2_m	R^2_c
Ant species richness	~ distance* + flower diversity *** + habitat *** + distance: flower diversity + distance: habitat + flower diversity: habitat **	915.9	1.4	71.7	0.150	0.196
	Model equation: $Y= e^{-1.289 - 0.718 \times D + 0.301 \times FD + 1.342 \times NV + 0.385 \times FD: NV}$					
Ant species richness (second best model)	~ distance* *+ flower diversity *** + habitat *** + flower diversity: habitat ***	917.3			0.138	0.179
	Model equation: $Y= e^{-1.471 - 0.309 \times D + 0.342 \times FD + 1.927 \times NV + 0.186 \times FD: NV}$					
Ant abundance	distance*** + habitat + flower diversity * distance: habitat ***	3277.892	7.542	12.199	0.066	0.066
	Model equation: $Y = e^{0.167 - 0.008 \times D + 0.126 \times FD + 0.0096 \times D: NV}$					
Flying visitor species richness	~ distance* + flower diversity *** + habitat *** + distance: flower diversity***	1785.7909	12.402	150.065	0.232	0.374
	Model equation: $Y= e^{-0.317 - 0.001 \times D + 0.392 \times FD - 1.114 \times NV - 0.001 \times D: FD}$					
Flying visitor abundance	~ distance *** + habitat *** + flower diversity *** + distance: habitat *** +	5044.422	238.916	245.543	0.186	0.193

distance: flower diversity ***+

habitat: flower diversity ***

Model equation: $Y= e^{1.609 + 0.14 \times D + 4.201 \times NV + 0.518 \times FD - 0.007 \times D: NV + 0.004 \times D: FD + 1.148 \times NV: FD}$

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*, < 0.05; **, <0.01; ***, <0.001

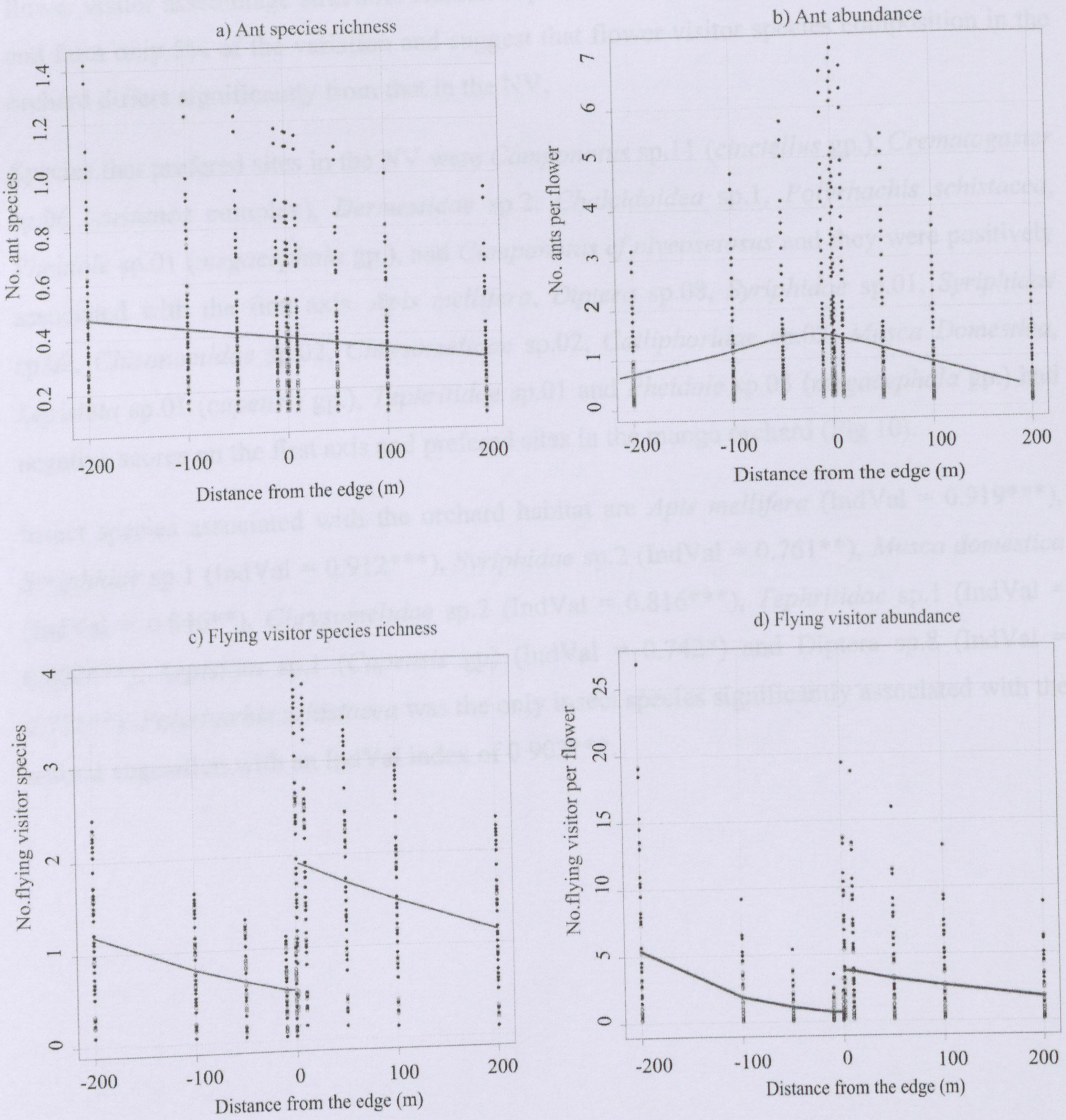


Figure 9 The effect of distance on ant and flying flower visitor abundance for all three farms used in this study (Fitted GAM model). Negative distance values represent distances into the

NV, away from the edge and positive values represent distances into the mango orchard (see Table 3 for details).

4.1.2.2 Flower visitor species composition

Distance did not have a significant effect on flower visitor species assemblage structure (P = 0.489). The first two axes of the redundancy analysis explained 29% of the variation in flower visitor assemblage structure. Habitat explained a large amount of the variation (24 %) and farm only 5% of the variation and suggest that flower visitor species composition in the orchard differs significantly from that in the NV.

Species that prefered sites in the NV were *Camponotus* sp.11 (*cinctellus* gp.), *Crematogaster* sp.06 (*custanea* complex), *Dermestidae* sp.2, *Chalcidoidea* sp.1, *Polyrhachis schistacea*, *Pheidole* sp.01 (*megacephala* gp.), and *Camponotus cf niveosetosus* and they were positively associated with the first axis. *Apis mellifera*, *Diptera* sp.08, *Syriphidae* sp.01, *Syriphidae* sp.02, *Chironomidae* sp.02, *Chrysomelidae* sp.02, *Calliphoridae* sp.02, *Musca Domestica*, *Lepisiota* sp.01 (*capensis* gp.), *Tephritidae* sp.01 and *Pheidole* sp.03 (*megacephala* gp.) had negative scores on the first axis and prefered sites in the mango orchard (Fig 10).

Insect species associated with the orchard habitat are *Apis mellifera* (IndVal = 0.919***), *Syriphidae* sp.1 (IndVal = 0.912***), *Syriphidae* sp.2 (IndVal = 0.761**), *Musca domestica* (IndVal = 0.846**), *Chrysomelidae* sp.2 (IndVal = 0.816***), *Tephritidae* sp.1 (IndVal = 0.802***), *Lepisiota* sp.1 (*Capensis* gp) (IndVal = 0.742*) and Diptera sp.8 (IndVal = 0.721**). *Polyrhachis schistacea* was the only insect species significantly associated with the natural vegetation with an IndVal index of 0.902***.

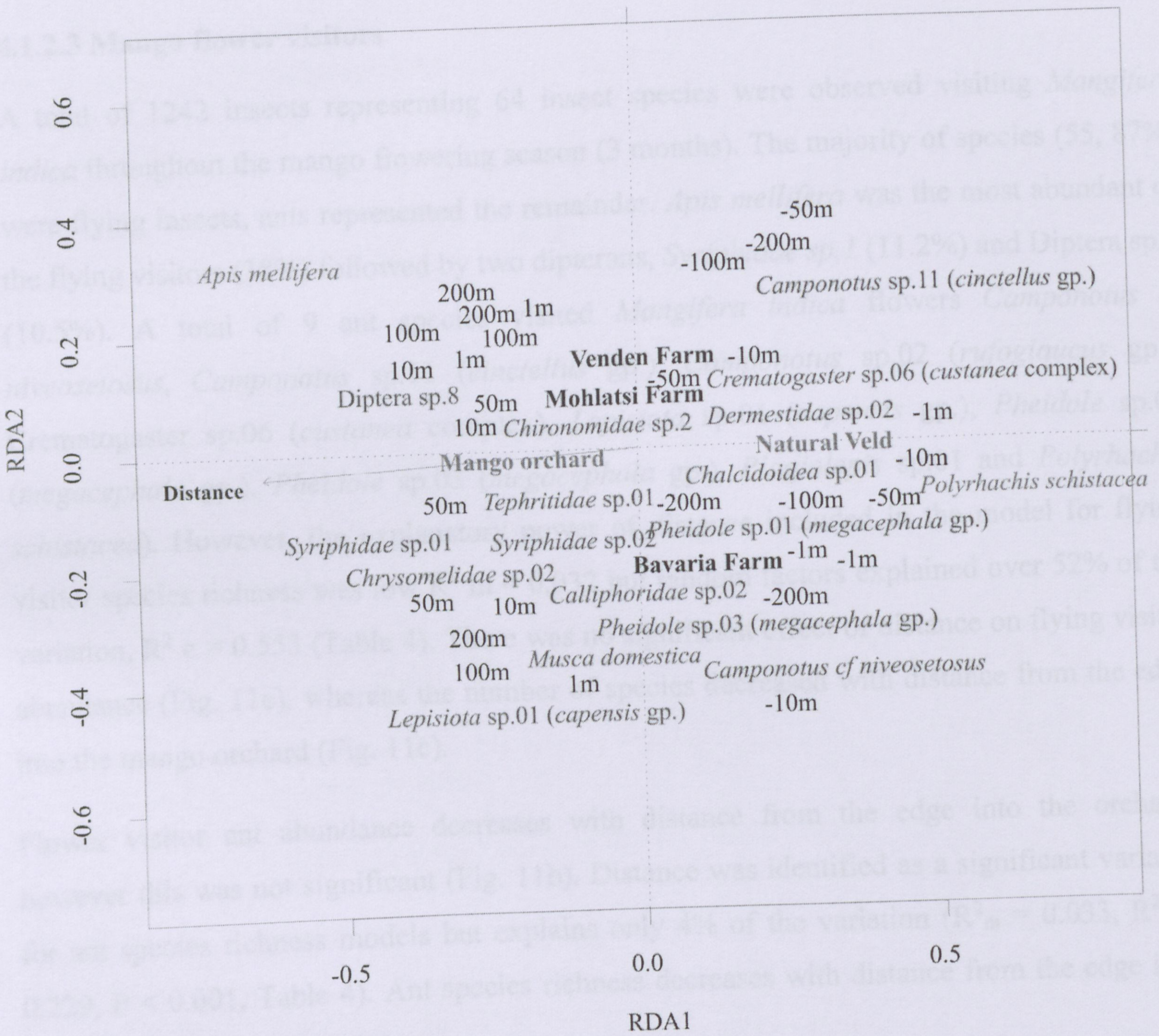


Figure 10 RDA ordination (biplot, sample scaling) of flower visitor assemblages.

4.1.2.3 Mango flower visitors

A total of 1242 insects representing 64 insect species were observed visiting *Mangifera indica* throughout the mango flowering season (3 months). The majority of species (55, 87%) were flying insects, ants represented the remainder. *Apis mellifera* was the most abundant of the flying visitors (38%) followed by two dipterans, *Syriphidae sp.1* (11.2%) and Diptera sp.8 (10.5%). A total of 9 ant species visited *Mangifera indica* flowers *Camponotus cf niveosetosus*, *Camponotus* sp.11 (*cinctellus* gp.), *Camponotus* sp.02 (*rufoglaucus* gp.), Crematogaster sp.06 (*custanea* complex), *Lepisiota* sp.01 (*capensis* gp.), *Pheidole* sp.01 (*megacephala* gp.), *Pheidole* sp.03 (*megacephala* gp.), *Plagiolepis* sp.01 and *Polyrhachis schistacea*). However, the explanatory power of distance included in the model for flying visitor species richness was low R^2 m = 0.032 but random factors explained over 52% of the variation, R^2 c = 0.553 (Table 4). There was no significant effect of distance on flying visitor abundance (Fig. 11c), whereas the number of species decreased with distance from the edge into the mango orchard (Fig. 11c).

Flower visitor ant abundance decreases with distance from the edge into the orchard; however this was not significant (Fig. 11b). Distance was identified as a significant variable for ant species richness models but explains only 4% of the variation (R^2_m = 0.033, R^2_c = 0.229, $P < 0.001$, Table 4). Ant species richness decreases with distance from the edge into the mango orchard (Fig. 11a).

Table 4 GLMM with Poisson distribution error showing the effect of distance from the edge into mango orchard and the presence of managed honey bee hives on mango flower visitor abundance and species richness. The change in AICc (ΔAIC) between the best model and the next best and worst are also given. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random effects, are given.

Response	Model	AIC (best model)	ΔAIC (second best)	ΔAIC (worst)	R2m	R2c
Ant species richness	~ distance*	296.2	1.7	4.4	0.033	0.229
	Model equation: $Y = e^{-254 - 0.284 \times D}$					

Ant species richness (second best model)	~ distance* + MHB	297.9			0.039	0.229
	Model equation: Y= e $^{-1.309 - 0.284 \times D}$					
Ant abundance	~ distance + MHB* + distance : MHB	171.0	1.1	3	0.013	0.013
	Model equation: Y= e $^{-4.862 + 2.821 \times MHB}$					
Ant abundance (second best model)	~ distance** + MHB	172.1			0.012	0.012
	Model equation: Y= e $^{-4.740 -0.859 x D}$					
Flying visitor species richness	~ distance*** + MHB + distance : MHB**	652.3	3.7556	5.713	0.032	0.553
	Model equation: Y= e $^{0.314 - 0.007 \times D + 0.006 \times D:MHB}$					
Flying visitor abundance	~ distance	370.1	2	3.3522	0.0007	0.330

*, < 0.05; **, <0.01; ***, <0.001, MHB – Managed honey bees

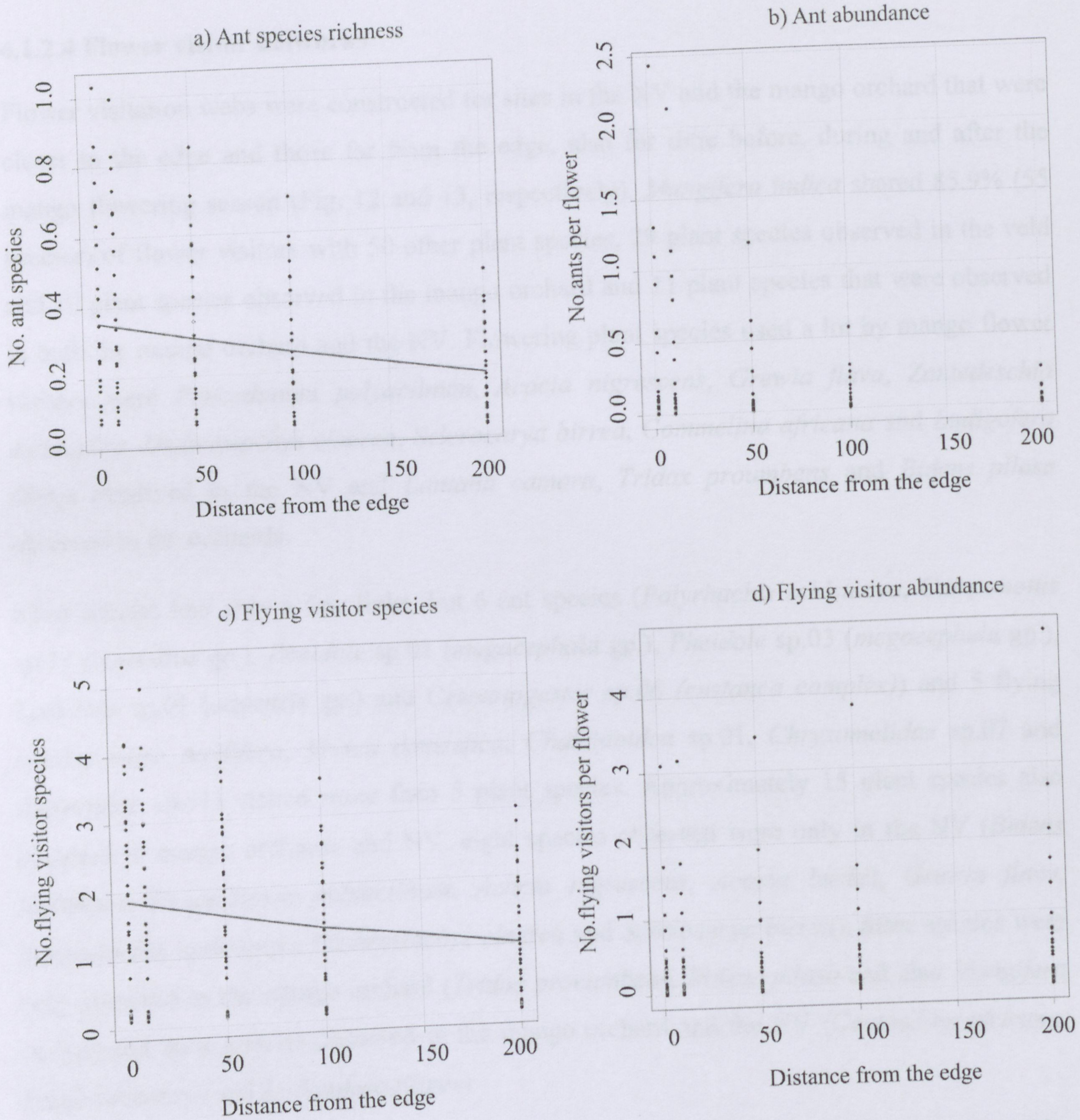


Figure 11 Scatter plots and fitted GAM models showing the effect of distance on *Mangifera indica* flower visitor abundance and species richness in the three farms from the edge of the mango orchard into the mango orchard (see Table 4 for statistical details).

4.1.2.4 Flower visitor networks

Flower visitation webs were constructed for sites in the NV and the mango orchard that were closer to the edge and those far from the edge, also for time before, during and after the mango flowering season (Fig. 12 and 13, respectively). *Mangifera indica* shared 85.9% (55 species) of flower visitors with 50 other plant species, 29 plant species observed in the veld and 10 plant species observed in the mango orchard and 11 plant species that were observed in both the mango orchard and the NV. Flowering plant species used a lot by mango flower visitors were *Peucedanum polyactinum*, *Acacia nigrescens*, *Grewia flava*, *Zantedeschia aethiopica*, *Dichrostachys cinerea*, *Sclerocarya birrea*, *Commelina africana* and *Ludigofera filipes* observed in the NV and *Lantana camara*, *Tridax proumbens* and *Bidens pilosa* observed in the orchards.

Most species had only a few links, but 6 ant species (*Polyrhachis schistacea*, *Camponotus sp.11 (cinctellus gp.)*, *Pheidole* sp.01 (*megacephala* gp.), *Pheidole* sp.03 (*megacephala* gp.), *Lepisiota* sp.01 (*capensis* gp.) and *Crematogaster sp.06 (custanea complex)*) and 5 flying species (*Apis mellifera*, *Musca domestica*, *Chalcidoidea* sp.01, *Chrysomelidae* sp.07 and *Reduviidae* sp.01) visited more than 5 plant species. Approximately 15 plant species also occurred in mango orchards and NV, eight species observed were only in the NV (*Bidens bipinnata*, *Peucedanum polyactinum*, *Acacia nigrescens*, *Acacia burkei*, *Grewia flava*, *Zantedeschia aethiopica*, *Dichrostachys cinerea* and *Sclerocarya birrea*), three species were only observed in the mango orchard (*Tridax procumbens*, *Bidens pilosa* and also *Mangifera indica*) and three species observed in the mango orchard and the NV (*Commelina africana*, *Lantana camara* and *Ludigofera filipes*)

There are more links in the flower visitor webs in the mango orchard than webs in the NV. Flower visitor webs in the mango orchard are more connected and nested than those in the NV. Flower visitor webs in the NV were more compartmentalized with three compartments far from the edge and four compartments closer to the edge. Flower visitor webs in the mango orchard, however, had one compartment each (Table 5). Flower visitor webs during the mango flowering season had the highest linkage diversity, followed by flower visitor webs before mango flowering season. Before and during mango flowering season, flower visitor webs were more connected than flower visitor webs after mango flowering season. The flower visitor web before mango flowering season had 6 compartments and flower visitor webs during and after mango flowering season also had one compartment each (Table 6).

Table 5 Network properties for distance from the edge. Negative values indicate distances into NV, positive values are those into orchards.

	Distance from the edge			
Network parameter	-200m to -100m	-10m to -1m	1m to 10m	100m to 200m
Connectance	0.07	0.07	0.16	0.16
Nestedness	9.26	7.78	10.9	12.48
Number of compartments	3	4	1	1
Linkage diversity	3.78	3.03	8.37	6.8

Table 6 Network properties for *Mangifera indica* flowering seasons.

	Mangifera indica flowering season		
Network parameter	Before	During	After
Connectance	0.11	0.11	0.07
Nestedness	16.98	5.53	6.19
Number of compartments	6	1	1
Linkage diversity	3.13	13.1	9.76

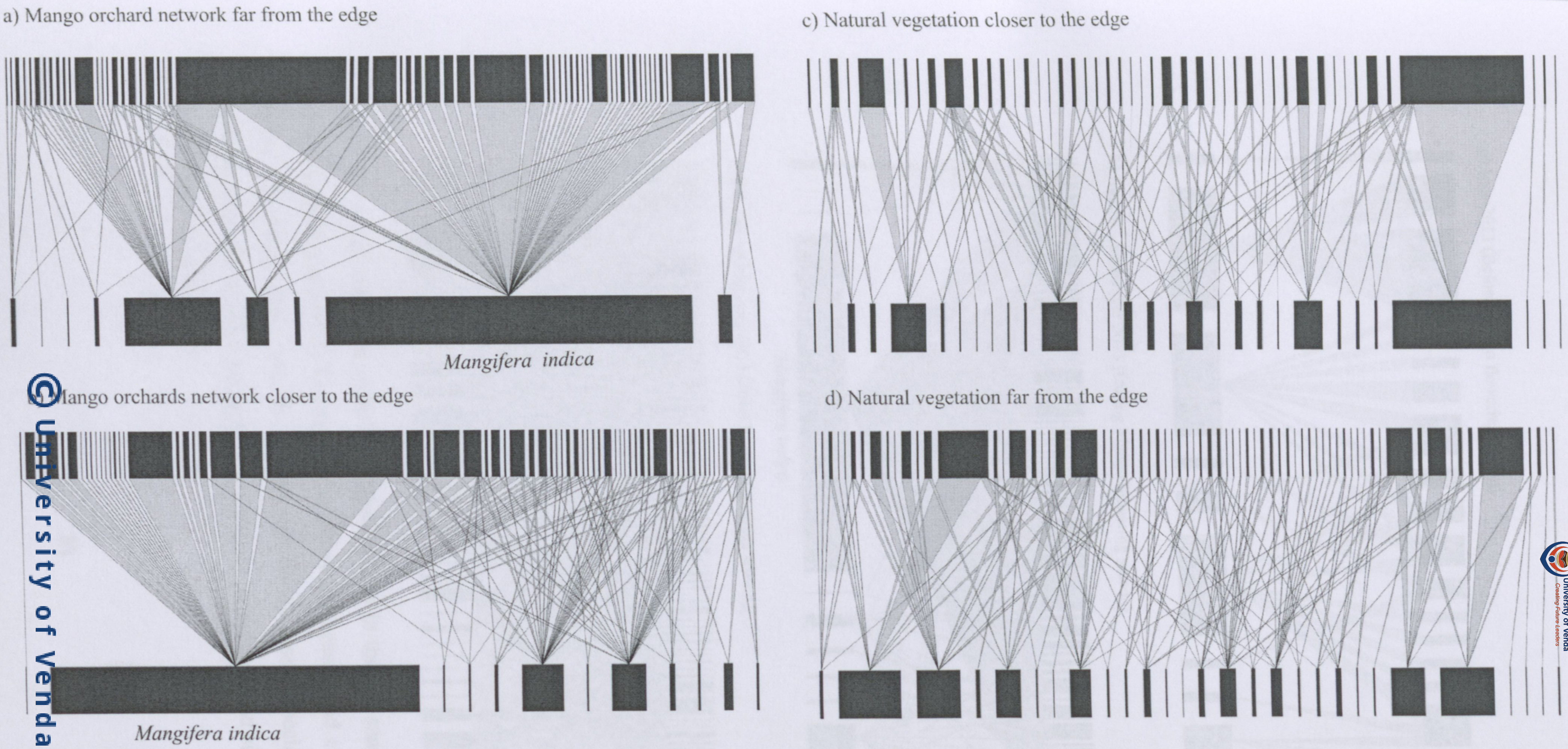
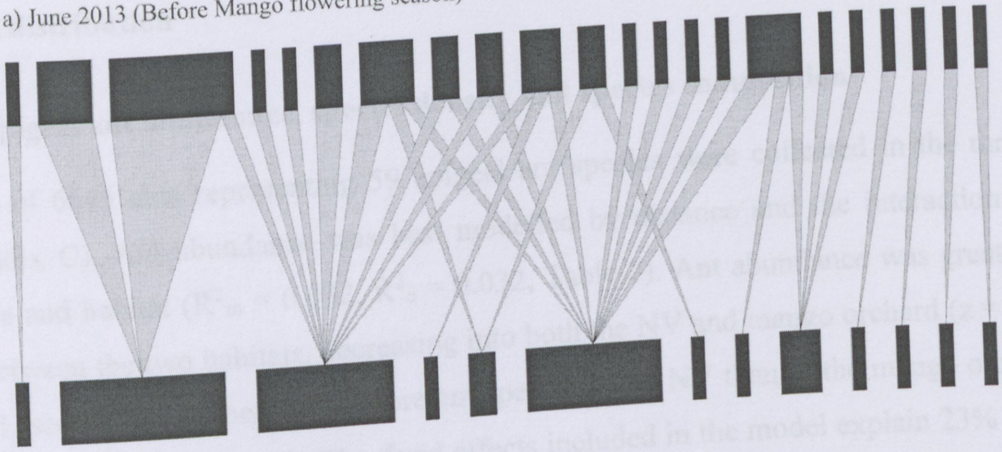
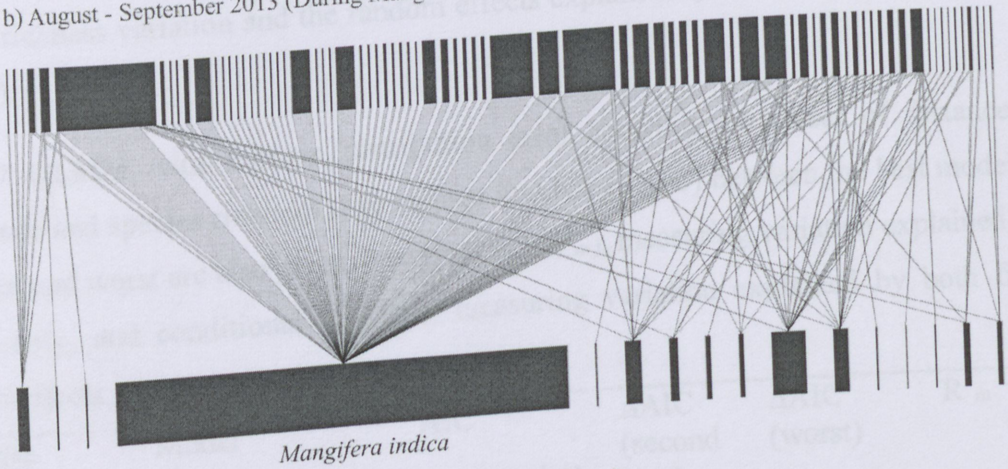


Figure 12 Flower visitation webs from observations in the six sampling months. a) Mango orchard far from the NV (100 m to 200 m away) b) Mango orchard closer to the NV(1 m to 10 m away) c) NV closer to the orchards (1 m to 10 m away) d) NV far from orchards (100 m to 200 m away). Flowering plant species and flower visitor insect species are represented by a rectangle, with the width representing the species abundance and size of the lines indicating the frequency of interaction. The list of flowering plants species and flower visitor species is provided in Appendix A and B, respectively.

a) June 2013 (Before Mango flowering season)



b) August - September 2013 (During Mango flowering season)



c) October and January 2013 (After Mango flowering season)

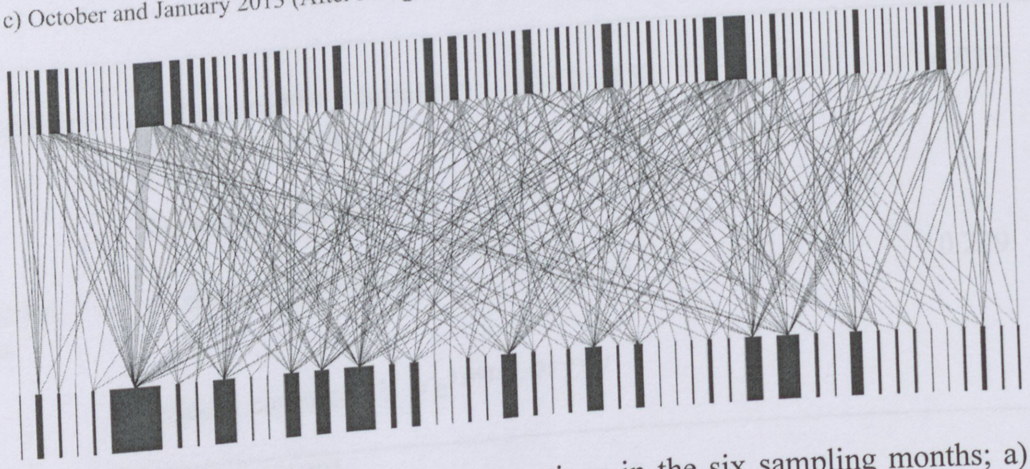


Figure 13 Flower visitation webs from observations in the six sampling months; a) Before mango flowering season b) During mango flowering season and c) After mango flowering season. Flowering plant species and flower visitor insect species are represented by a rectangle, with the width representing the species abundance and size of the lines indicating the frequency of interaction.

4.2 Ant distribution

4.2.1 Epigeal ant abundance, species density and species composition

A total of 6645 ants representing 59 epigeal ant species were collected in the three farms (Appendix C). Ant abundance was best modelled by distance and the interaction between distance and habitat ($R^2_m = 0.032$, $R^2_c = 0.032$, Table 7). Ant abundance was greatest at the edge between the two habitats, decreasing into both the NV and mango orchard ($z = -10.36$, $P < 0.001$, see Fig. 14). There were more ant species in the NV than in the mango orchard ($z = 4.006$, $P < 0.001$, see Fig. 15). The fixed effects included in the model explain 23% of the ant species richness variation and the random effects explain only 6% ($R^2_m = 0.229$, $R^2_c = 0.291$, Table 7).

Table 7 GLMM with Poisson distribution error showing the effect of distance on ant abundance and species richness. The change in AICc (ΔAIC) between the best model and the next best and worst are also given. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random effects, are given

Response	Model	AIC (best model)	ΔAIC (second best)	ΔAIC (worst)	R^2_m	R^2_c
Ant abundance	~ distance*** + habitat + distance : habitat*** Model equation: $Y = e^{4.308 - 0.003 \times D + 0.004 \times D:NV}$	5163	152	154	0.032	0.032
Ant species richness	~ distance + habitat*** Model equation: $Y = e^{1.691 + 0.435 \times NV}$	492	2	14	0.229	0.291

*, < 0.05; **, <0.01; ***, <0.001

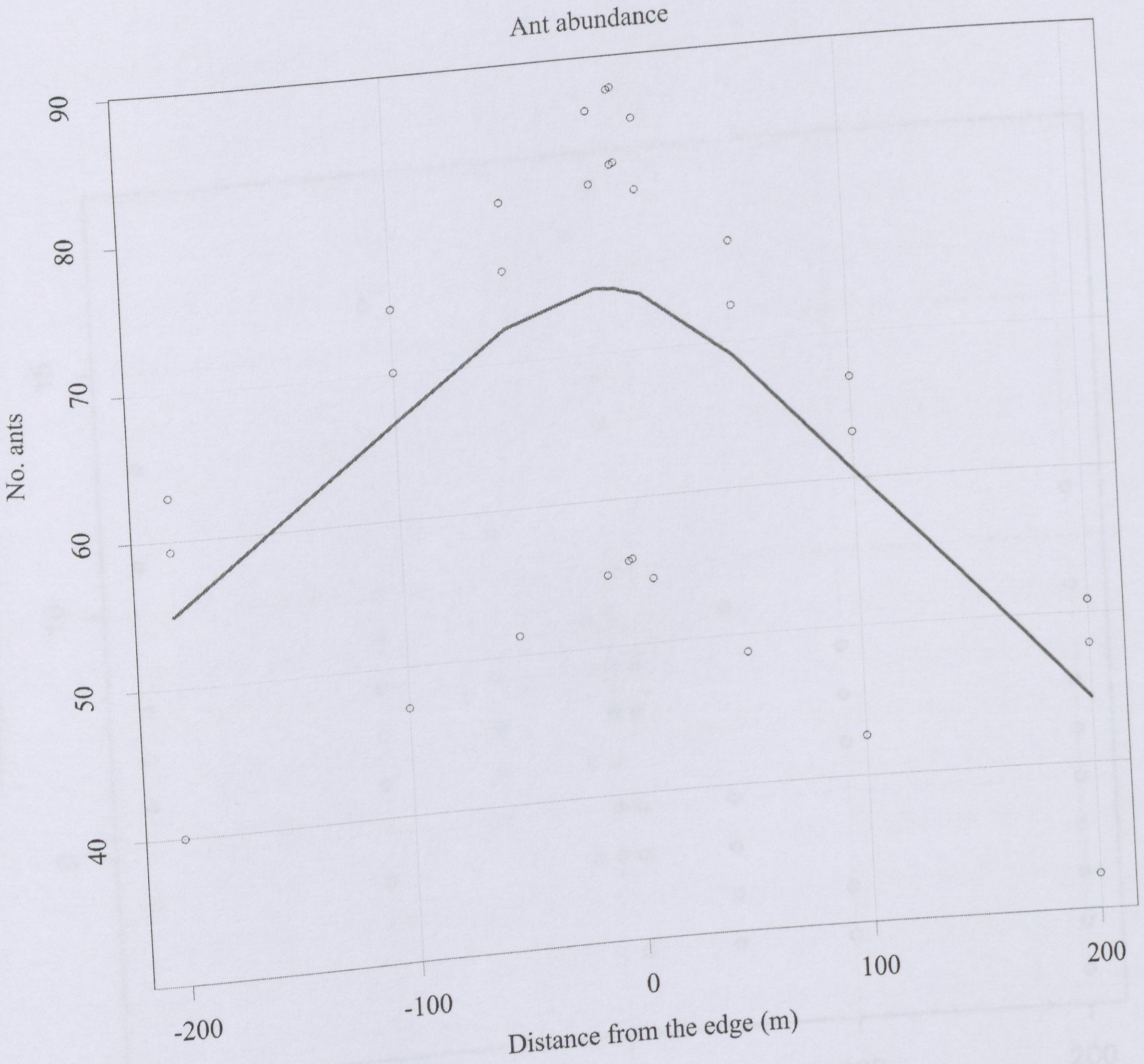


Figure 14 Scatterplot and fitted model (GAM) summarizing the effect of distance on ant abundance from the edge into the NV and mango orchards(Table 7).

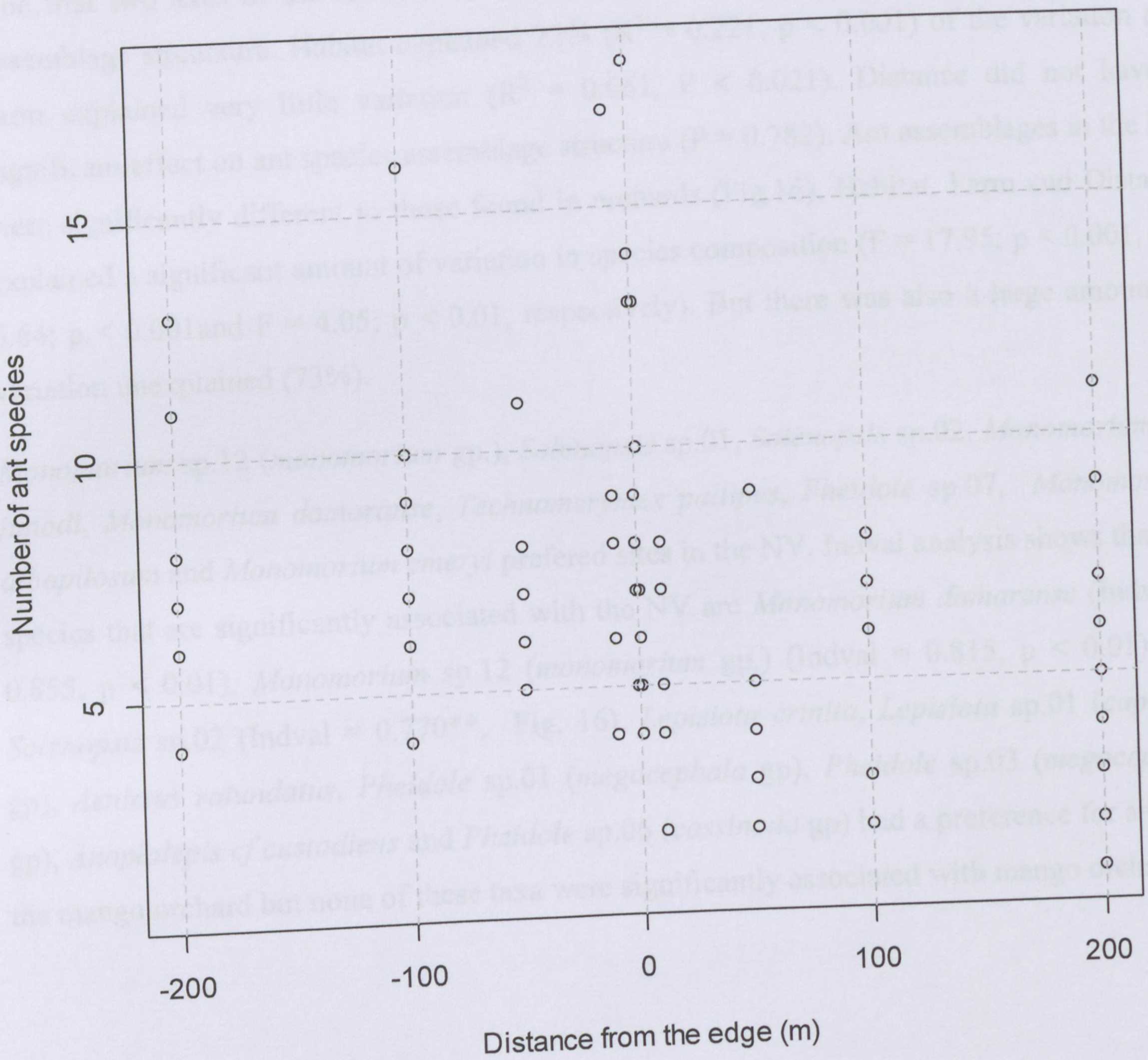


Figure 15 Scatter plots summarizing the effect of distance on ant species richness in Bavaria, Mohlatsi and Venden farms from the edge of the mango orchard into the mango orchard (see Table 7 for statistical values).

4.2.2 Ant species composition

The first two axes of the redundancy analysis explained 28% of the variability in species assemblage strcucture. Habitat explained 22% ($R^2 = 0.221$, $p < 0.001$) of the variation and farm explained very little variation ($R^2 = 0.061$, $P < 0.021$). Distance did not have a significant effect on ant species assemblage structure ($P = 0.782$). Ant assemblages in the NV were significantly different to those found in orchards (Fig.16). Habitat, Farm and Distance explained a significant amount of variation in species composition ($F = 17.95$; $p < 0.001$, $F = 6.64$; $p < 0.001$and $F = 4.05$; $p < 0.01$, respectively). But there was also a large amount of variation unexplained (73%).

Monomorium sp.12 (*monomorium* gp.), *Solenopsis* sp.01, *Solenopsis* sp.02, *Monomorium Cf. junodi*, *Monomorium damaranse*, *Technomerymex pallipes*, *Pheidole* sp.07, *Monomorium albopilosum* and *Monomorium emeryi* prefered sites in the NV. Indval analysis shows that the species that are significantly associated with the NV are *Monomorium damarense* (Indval = 0.855, $p < 0.01$), *Monomorium* sp.12 (*monomorium* gp.) (Indval = 0.815, $p < 0.01$) and *Solenopsis* sp.02 (Indval = 0.770**, Fig. 16). *Lepisiota crinita*, *Lepisiota* sp.01 (*capensis* gp), *Aenictus rotundatus*, *Pheidole* sp.01 (*megacephala* gp), *Pheidole* sp.03 (*megacephala* gp), *Anoplolepis cf custodiens* and *Pheidole* sp.06 (*cassinoda* gp) had a preference for sites in the mango orchard but none of these taxa were significantly associated with mango orchards.

Figure 16 RDA ordination (biplot, sample scaling) of ant assemblages

4.2.3 Which ant species were the most dominant and how did their abundance change with distance from the edge?

Pheidole sp.03 (*megacephala* gp.) (36%), *Pheidole* sp.01 (*megacephala* gp.) (13%), *Monomorium cf junodi* (10%), *Monomorium damarense* (6%) were the most dominant epigeal ants. The best model for *Pheidole* sp.03 (*megacephala* gp.), *Pheidole* sp.01 (*megacephala* gp.) and *Monomorium damarense* identified distance, habitat and the interaction between distance and habitat as fixed effects that explained a large amount of variation ($R^2_m = 0.242$, $R^2_c = 0.242$; $R^2_m = 0.078$, $R^2_c = 0.078$ and $R^2_m = 0.317$, $R^2_c = 0.468$, respectively, see Table 8). *Pheidole* sp.03 (*megacephala* gp.) and *Pheidole* sp.01 (*megacephala* gp.) abundance decreased with distance from the edge in both the mango orchard and the NV ($z = 14.027$, $P < 0.001$ and $z = 9.264$, $P < 0.001$, see Fig. 18). The effect of distance on the abundance of *Monomorium damarense* was greater in the mango orchard than in the NV. *Monomorium cf junodi* was best explained by distance and habitat with an R^2_m 0.107 and an $R^2_c = 0.107$ (see Table 8). *Monomorium cf. junodi* abundance increased from the edge into the NV and decreased with distance from the edge into the mango orchard, ($z = 3.701$, $P < 0.001$ and $z = 3.824$, $P < 0.001$, see Fig. 17).

Table 8 GLMM with Poisson distribution error showing the effect of distance from the edge into mango orchard on abundant ant species. The change in AICc (ΔAIC) between the best model and the next best and worst are also given. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random effects, are given.

Response	Model	AIC (best model)	ΔAIC (second best)	ΔAIC (worst)	R2m	R2c
Pheidole sp.03 (*megacephala*)	~ distance*** + habitat*** + distance : habitat***	4910.054	482.6	954.856	0.242	0.242
	Model equation: $Y = e^{3.535 - 0.005 \times D - 0.808 \times NV + 0.019 \times D:NV}$					
Pheidole sp.01 (*megacephala*)	~ distance*** + habitat*** + distance : habitat***	1867.3831	47.8184	166.7149	0.078	0.078

	Model equation: $Y = e^{2.769 - 0.005 \times D - 0.899 \times NV + 0.008 \times D:NV}$					
Monomorium cf junodi	~ distance*** + habitat*** + distance : habitat***	1551.3	0.9245	71.7	0.107	0.107
	Model equation: $Y= e^{0.779 - 0.006 \times D + 0.983 \times NV}$					
Monomorium cf junodi (second best model)	~ distance*** + habitat***	1552.2			0.105	0.105
	Model equation: $Y = e^{0.647 - 0.004 \times D + 1.085 \times NV}$					
Monomorium damarense	~ distance*** + habitat*** + distance : habitat***	652.3665	16.9586	84.7194	0.317	0.468
	Model equation: $Y = e^{0.268 - 0.013 \times D + 1.079 \times NV + 0.012 \times D:NV}$					

*, < 0.05; **, <0.01; ***, <0.001

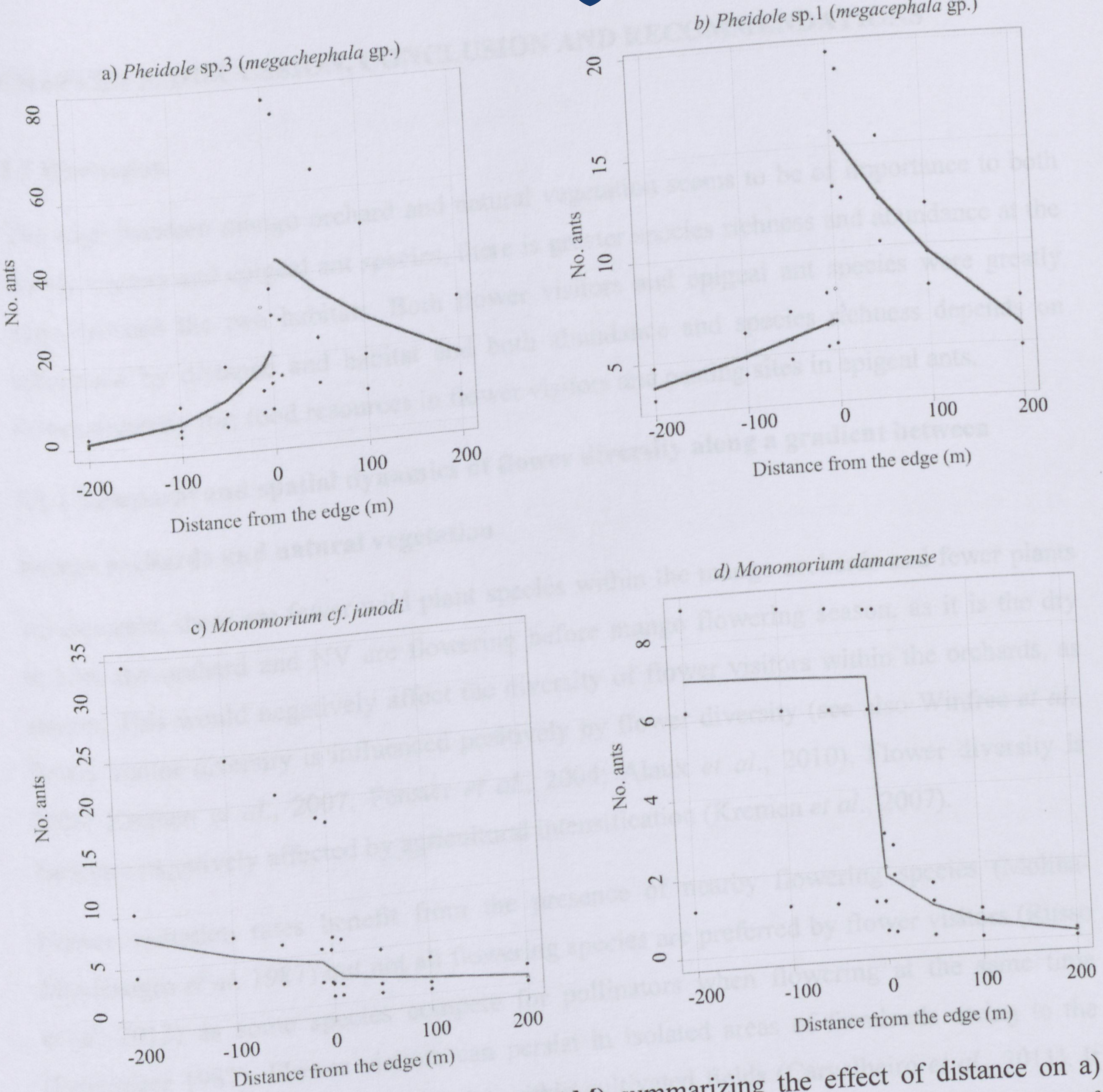


Figure 17 Size plots and fitted model (GAM) summarizing the effect of distance on a) *Pheidole* sp.03 (*megacephala* gp.), b) *Pheidole* sp.01 (*megacephala* gp), c) *Monomorium cf. junodi* and d) *Monomorium damarense* abundance in Bavaria, Mohlatsi and Venden farms from the edge of the mango orchard into the mango orchard.

CHAPTER 5: DISCUSSION, CONCLUSION AND RECOMMENDATIONS

5.1 Discussion

The edge between mango orchard and natural vegetation seems to be of importance to both flower visitors and epigeal ant species, there is greater species richness and abundance at the edge between the two habitats. Both flower visitors and epigeal ant species were greatly influenced by distance and habitat and both abundance and species richness depends on flower diversity for; food resources in flower visitors and nesting sites in epigeal ants.

5.1.1 Temporal and spatial dynamics of flower diversity along a gradient between mango orchards and natural vegetation

As expected, there are fewer wild plant species within the mango orchards and fewer plants in both the orchard and NV are flowering before mango flowering season, as it is the dry season. This would negatively affect the diversity of flower visitors within the orchards, as flower visitor diversity is influenced positively by flower diversity (see also Winfree *et al.*, 2008; Kremen *et al.*, 2007; Fenster *et al.*, 2004; Alaux *et al.*, 2010). Flower diversity is therefore negatively affected by agricultural intensification (Kremen *et al.*, 2007).

Flower visitation rates benefit from the presence of nearby flowering species (Molina-Montenegro *et al.* 1987) but not all flowering species are preferred by flower visitors (Russo *et al.* 2013) as some species compete for pollinators when flowering at the same time (Feinsinger 1987). Flower visitors can persist in isolated areas of farmlands owing to the presence of ruderal plants (i.e., weeds) within cultivated fields (Carvalheiro *et al.*, 2011). It will however be important to study if these plants would compete for resources with mango trees. Although weeds were important during mango flowering, there were a number of native plant species within the natural vegetation that were important for flower visitors when mango was not flowering, highlighting the value of observing pollinator networks over time, and also highlighting the importance of natural species to supporting the pollinator network throughout the year.

5.1.2 Temporal and spatial dynamics of flower visitor diversity along a gradient between mango orchards and natural vegetation

A diverse community of ant and flying flower visitors visited *Mangifera indica* during the peak of the mango flowering season (Fig. 8). There is a positive relationship between flying flower visitor richness and plant diversity. An increase in the abundance of wild flower resources in the NV and inside the mango orchard (August – September) may have facilitated the increase in Mango flower visitation or this could be because a result of the great abundance of mango flowers whilst mango was flowering boosting flower visitor populations.

Ants and flying flower visitors seem to be effective mango pollinators (Carvalheiro *et al.* 2010). Although the number of flying visitor species increased by 27% after mango flowering season, their abundance decreased by over 56%. Unlike flying visitors, ant species richness and abundance increased even more after the mango flowering season. Ants can also have negative effects on seed set, but when their visitation rate is high or in the absence of flying flower visitors they may have the greatest impact as pollinators (Ashman and King, 2005).

Both ant and flying visitor species richness were influenced by distance from the edge between the two habitats, and habitat type. There is a clear decline in flower visitor abundance and species richness with distance from the edge towards the mango orchard, consistent with findings by other authors (Ricketts *et al.*, 2008, Krewenka *et al.*, 2011 and Carvalheiro *et al.*, 2010). Flower resources for mango flower visitors can be supplemented by planting native plant species or weeds flowering throughout the year within mango orchards (Carvalheiro *et al.* 2011; Carvalheiro *et al.*, 2012; Morandin and Winston 2006). The diversity of flower visitors in the NV owing to a diverse community of flowering plant species suggest that maintaining and/or introducing some of these native plant species within the mango orchard will benefit the diversity of mango flower visitors (see also Winfree *et al.*, 2008).

Croplands are usually irrigated and/or fertilised, so tend to be more productive than the surrounding environment. Given that organisms usually move from high to low productivity systems (Tscharntke *et al.* 2005), flower visitor movement from croplands into natural vegetation would be expected. However, ants and flying visitors were more abundant at the edge between the natural vegetation and the mango orchard (Fig.9). Habitat edges can be distinctive habitat types that enable distinct species interactions (Fagan et al., 1999). Species that thrive in anthropogenic disturbances (Dauber, 1997), like many ant species are abundant at edges (Dauber and Wolters, 2004). Carvalheiro *et al*. (2010) found that the negative impact of distance to natural vegetation on flower visitor abundances cannot be ameliorated by large percentages of natural vegetation surrounding mango orchards, i.e, field size was a far better predictor of flower visitor abundance than percentage natural vegetation in the near vicinity. Their study suggested that smaller orchards are more preferable to increase flower visitation (see also Tscharntke *et al*., 2005; Kremen *et al*., 2007). Alternatively, farmers should consider an active management of hedgerows at the edges and within orchards with plants flowering before and after mango flowering season to increase flower visitation (see also Winfree *et al*., 2008 and Carvell *et al*., 2004). These patches would also provide nesting sites for pollinators. Design elements that increase edge to area ratios in orchards, or at least, smaller mango fields, should be able to increase flower visitation.

Although distance explained the variation in flower visitor abundance and species richness, it didn't explain assemblage composition. *Polyrhachis schistacea* was the only flower visitor species identified as an indicator species for sites in the NV. This species prefer a variety of nesting site including arboreal and epigeal nests (Munyai and Foord, 2012). Variation of flower visitor assemblage with distance from the edge is more pronounced in the mango orchard compared to the NV (Fig.11). The results show that *Apis mellifera* was the most frequent flying flower visitor in mango flowers regardless of the fact that mango flowers are not very attractive to honeybees (Free and Williams, 1976). *Apis mellifera* was not affected by the negative effect of distance on flower visitor abundance, as it was also abundant in sites furthest from the NV. This could have been because bee hives are placed within mango orchards at a density of 1 hive.ha^{-1} during mango flowering season, therefore, managed bees did not always have to travel far to reach mango flowers.

5.1.3 Spatial and temporal dynamics of flower visitor networks

Mangifera indica shares 85% of its flower visitors with 50 other plant species. It is therefore assumed that these plant species are important flower resources for mango flower visitors before and after mango flowering season. Flowering plants visited by mango flower visitors after mango has ceased flowering include *Peucedanum polyactinum*, *Acacia nigrescens*, *Grewia flava*, *Zantedeschia aethiopica*, *Dichrostachys cinerea*, *Sclerocarya birrea*, *Commelina africana* and *Ludigofera filipes*. Plant species supporting mango flower visitors before, during and after mango flowering season are *Lantana camara* (observed flowering June and later in January), *Tridax proumbens*, *Bidens pilosa* (flowering throughout the sampling period). Notably, these species are introduced weed species, found in high densities in disturbed areas. Their presence within mango orchards in close proximity to mango flowers might explain their importance to mango flower visitors. Diversity of plant species with different phenologies could ensure that there is flower resource for pollinators before and after mango flowering season.

Flower visitor webs in the mango orchards contained more links than the webs in the NV, with higher linkage diversity in webs found at sites closer to the edge. This suggests that flower visitation tends to be higher in sites closer to the edge than those far from the edge. Connectance is also higher in the mango orchard. Higher connectance implies that the interactions between species are more generalist. Generalist species are able to thrive on different species for resources and not just a specific species. Connectance represents the proportion of all possible links in food webs (Fontaine *et al*., 2011). Flower visitor webs in the mango orchards are fully connected, implying that these networks are unstable (Stouffer and Bascompte, 2011). Lower connectance (giving the impression of greater specialisation) can also arise if there are very few observations, or if there are a number or rare species within a sample (Blüthgen 2010). This may have been the case here, as natural vegetation had a greater diversity of plant species which were visited relatively rarely compared to plant species within the mango orchards. This could also be a result of low diversity in flower resources that are nevertheless abundant in the orchards. *Mangifera indica* is the most abundant flower resource in the mango orchard, providing flower resources for insect communities during its flowering season. Connectance of flower visitor webs in the mango orchards suggest that flower visitation will collapse within the mango orchards after *Mangifera indica* has ceased flowering. But contrary to this, the results indicate that ant abundance, ant species richness and flying visitor species richness increase after mango flowering season in both the mango orchard and the NV (Fig 8a, 8b and 8c). This increase is largely the result of increased temperatures during the latter part of the study (summer conditions). Flying visitor abundance seems to decrease when mango ceased flowering (Fig 8d).

Compartments buffer the propagation of extinction. Stouffer and Bascompte (2011) discuss that the inhibition of disturbances within compartments positively affects community persistence. Our results reveal that flower visitor webs in the NV are compartmentalized suggesting that they are more stable than flower visitor webs in the mango orchards. The flower visitor web before mango flowering season also seems to be more stable than flower visitor webs during and after mango flowering season. A stable community is resilient to species extinction due to fewer fluctuations in visitation populations over time.

5.1.4 Ant distribution

There was no clear pattern of epigeal ant species richness with distance from the edge, but the edge seems to be important for ant abundance just as in flower visitor abundance (see also Brandao *et al*., 2011). Ant species richness has been found to be higher in open habitats that are less complex (Andersen, 1995; Sanders, 2002; Dunn *et al*., 2009; Munyai and Foord, 2012). Ant species that are habitat generalists, or non-native, and species that prefer open areas are most likely to be abundant at the edges (Schoereder *et al*., 2004; Brandao *et al*., 2011). Ant assemblages also differed significantly between NV and mango habitats, probably because of the markedly different thermal environments and habitat characteristics of the two habitats.

Other studies show the importance of connections with other plant species on ant tending and visitation by creating foraging trails (Bentley 1981; Apple and Feener, 2001). Habitat disturbance increases habitat heterogeneity which would increase ant diversity (Wisdom and Whitford, 1981; Ewers and Didham, 2008). Ants prefer plants with the most rewarding nectar sources (Apple and Feener, 2001), the declining ant abundance in this study could be associated with the decreased number of plant species for foraging trails and/or absence of preferred nectar sources in the orchard. There is therefore need to study the ant preference of *M. indica*'s nectar compared to other plant species.

The subfamilies with the highest diversity were Myrmicinae and Formicinae, with *Pheidole* sp.01 (*megacephala* gp.), *Pheidole* sp.03 (*megacephala* gp.), *Monomorium damarense* and *Monomorium cf. junodi*, all from the Myrmicinae subfamily, as numerically most abundant ant species. Ant species in these two families have their nests in different habitats ranging from soil, and arboreal in tree trunks and twigs (Shattuck, 1999). Species in the *Pheidole* and *Monomorium* genera are well known as dominant ant taxa in Africa (Andersen, 1993).

The orchards and natural vegetation had distinct assemblages. Orchard did not have any indicator species but was associated with two of the most abundant species in the farms, *Pheidole* sp.01 (*megacephala* gp.) and *Pheidole* sp.03 (*megacephala* gp.). Ant communities with low species diversity are able to protect plant species in the presence of a single dominant species with high abundance (Weilgoss *et al*., 2014). *Pheidole megacephala* group do best in relatively disturbed habitats and thrive in cultivated land (Wilson, 2003) and due to its aggressive behaviour, it affects the other insects (Holldobler and Wilson, 1990). Munyai and Foord (2012) found that *Pheidole megacephala* was associated with cooler sites and higher vegetation cover. The absence of indicator species in mango orchards could be explained by the fact that generalist ant species tend to be associated with disturbed areas, and because most ant species in the mango orchard were also found in the NV.

Monomorium damarense and *Monomorium cf. junodi* were the most abundant ant species in the NV and sites closer to the edge. *Monomorium* genus is known to prefer hot and open habitats (Andersen, 1997; 2000). The species in the *Monomorium* genus ranges from scavenger and predators to seed harvesters differ in size and prefer a diverse range of habitats (Briese and Macauley, 1981). Temperature was not considered in this study but these species were found in sites with a presence of bare ground and high levels of solar insolation (Holldobler and Wilson, 1990).

Ant abundance decreased with distance from the edge towards the NV and the mango orchard (Fig.14). This correlates with observations by Andersen (2000) where structural complexity impedes ants from food resources due to leaf litter. Munyai and Foord (2012) also observed that ant species assemblage decreased with an increase in leaf litter and structural complexity. However, the quality of plant protection does not only depend on abundance of ants but also the identity of the tending ants (Apple and Feener, 2001). Krull (2004) suggested that epigeal ants play an important role in the control of pest insects in mango plantations. The aggressive and dominant traits of most ant species make them helpful in integrated pest management programs (Way and Khoo, 1992).

Distance from the edge did not significantly affect species richness and abundance, or species composition. Both GLMM in ant species and RDA analysis revealed habitat to be a significant variable explaining ant assemblage structure. Variation of ant species assemblage seems to be more pronounced in the NV than the orchard, likely because the habitat is more heterogeneous in NV (Fig. 16). Temperature also plays an important role in structuring ant communities (Zheng and Chen, 2000; Parr *et al*., 2005).

5.2 Conclusion

This study highlights the importance of edges as a design element in determining flower visitation in Mango orchards. Flower visitation tends to be higher in sites closer to the edge than those far from the edge, possibly because the edges contain elements of both habitats and because there are spill-over effects from the neighbouring habitat. Both ant and flying flower visitor species richness were influenced by distance from the edge and habitat type. The low diversity of flower resources in the mango orchards has a negative impact on mango flower visitors. Variation in flower visitor abundance and species richness were mostly explained by distance from the edge. *Polyrhachis schistacea* was the only NV indicator species, while 8 indicator species including *Apis mellifera* were observed in the mango orchard. This suggests that flower visitors in Mango orchards tend to be the same throughout, whereas there is considerable more variation in flower visitors across the study sites.

Mangifera indica shared most of its flower visitors with generalist plant species that make use of different flower resources from a variety of plant species. Flower visitors in the NV and those before mango flowering season have less fluctuations in their populations and are thus more stable than those in the mango orchards and those during and after mango flowering season.

The species abundance, richness and composition of epigeal ant species were different for each habitat. There was no clear pattern of epigeal ant species richness with distance from the edge. Ant abundance was high in disturbed sites closer to the edge and decreased with distance into the mango orchard and NV. Both GLMM in ant species and RDA analysis reveals habitat as a significant variable that explains ant assemblage. There were no indicator species in the mango orchard. Ant species variation was more pronounced in the mango orchard than the NV.

5.3 Recommendations

The diversity of flower visitors in the NV due to a diverse community of flowering plant species and the diversity and abundance of epigeal ants suggest that maintaining native plant species at different distance within the mango orchard may benefit the diversity and stability of mango flower visitors for pollination and epigeal ants for pest control.

Further studies using bagging experiments are important in determining which flower visitors are actually effective pollinators of mango. This may contribute significantly in understanding the role played by the different species of flower visitors' found in different distances from the NV towards the mango orchard. Another important study would be to use network analysis a step further and investigate what pollen is found on the different insect flower visitors.

The placement of mango orchards are typically due to logistical and horticultural reasons, making the layout of orchards and their edges with natural vegetation, difficult to change in practice in the study system. Follow up studies to show economic benefits of beneficial insects to farmers will likely be needed before orchard design will be changed in practice.

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Appendix A: A list of flowering plant species

Plant.no	Plant species	Mango fields	Natural vegetation	Total abundance
	Acanthaceae			
1	*Asystasia gangetica*	0	14	14
2	*Hypoestes forskaolii*	0	3	3
3	*Justicia flava*	7	4	11
4	*Justicia odora*	0	1	4
5	*Monechma debile*	0	3	3
	Anacardiaceae			
6	*Mangifera indica*	1294	0	1294
7	*Sclerocarya birrea*	0	22	22
8	*Searsia discolor*	0	48	48
	Apiaceae			
9	*Peucedanum polyactinum*	0	30	30
	Apocynaceae			
10	*Pentarrhinum insipidum*	0	14	14
	Araceae			
11	*Zantedeschia aethiopica*	0	13	13
	Asteraceae			
12	*Bidens pilosa*	2174	0	2174
13	*Bidens bipinnata*	0	13	13
14	*Epaltes gariepina*	0	9	9
15	*Galinsoga parviflora*	19	0	19
16	*Gnaphalium luteo-album* Linn.	1	0	1
17	*Osteospermum muricatum*	1	1	2
18	*Helichrysum candolleanum*	93	0	93
19	*Schkuhria pinnata*	38	2	40
20	*Sonchus oleraceus*	27	0	27
21	*Thymophylla tenuiloba var tenuiloba*	13	0	13
22	*Tridax procumbens*	2098	0	2098
23	*Vernonia fastigiata*	0	4	4
	Campanulaceae			
24	*Lobelia erinus*	0	4	4
	Commelinaceae			
25	*Commelina africana*	380	102	482

26	*Commelina eckloniana*	0	18	18
27	*Commelina erecta blue*	30	20	50
28	*Commelina erecta purple*	15	14	29
29	*Commelina erecta yellow*	10	3	13
	Convolvulaceae			
30	*Convolvulus sagittatus var aschersonii*	0	1	1
31	*Evolvulus alsinoides*	31	17	48
32	*Ipomoea bolusiana*	0	8	8
33	*Ipomoea obscura*	3	19	22
	Euphorbiaceae			
34	*Euphorbia hirta*	234	0	234
	Fabaceae			
35	*Acacia (Senegalia) burkei*	0	12	12
36	*Acacia (Vachellia) haematoxylon*	0	4	4
37	*Acacia (Vachellia) karroo*	0	90	90
38	*Acacia (Senegalia) polyacantha*	24	6	30
39	*Acacia (Senegalia) nigrescens*	0	104	104
40	*Acacia (Senegalia) senegalensis*	0	7	7
41	*Chamaecrista mimosoides*	3	0	3
42	*Chamaecrista comosa*	3	1	4
43	*Desmodium repandum*	0	8	8
44	*Dichrostachys cinerea*	0	8	8
45	*Indigastrum costatum subsp. Macrum*	10	0	10
46	*Indigofera filipes*	1	940	941
47	*Indigofera adenoides*	1	0	1
48	*Indigofera holubii*	0	15	15
49	*Acrotome hispida*	0	1	1
50	*Melilotus indicus*	0	7	7
51	*Microcharis galpinii*	1	0	1
52	*Tephrosia multijuga*	1	0	1
	Gentianaceae			
53	*Sabaea leiostyla*	0	48	48
	Geraniaceae			
54	*Monsonia angustifolia*			
55	*Monsonia glauca*			

	Lamiaceae			
56	*Becium obovatum*	3	94	97
57	*Crabbea acaulis*	0	1	1
	Malvaceae			
58	*Abutilon ramosum*	16	0	16
59	*Grewia flava*	0	109	109
60	*Pavonia burchelli*	1	0	1
61	*Sida cordifolia*	3	0	3
62	*Waltheria indica*	3	3	6
63	*Hibiscus pedunculatus*	0	1	1
	Meliaceae			
64	*Turraea obtusifolia*	5	0	5
	Oleaceae			
65	*Menodora africana*	0	1	1
	Oxalidaceae			
66	*Oxalis corniculata*	2	0	2
	Polygalaceae			
67	*Polygala uncinata*	0	1	1
	Portulacaceae			
68	*Portulaca quadrifida*	1	0	1
	Rubiaceae			
69	*Oldenlandia herbacea*	67	0	67
	Solanaceae			
70	*Solanum panduriforme*	0	2	2
	Sterculiaceae			
71	*Sterculia rogersii*	0	7	7
	Verbenaceae			
72	*Lantana camara*	2	193	195
73	*Lantana rugosa*	2	22	24
	Xanthorrhoeaceae			
74	*Aloe marlothii*	0	5	5
	Zygophyllaceae			
75	*Tribulus terrestris*	0	2	2

76	**Zingiberaceae** *Hedychium coronarium*	0	2	2

Appendix B: A list of flower visitor species

	Flower visitor species	Mango orchard	Natural vegetation	Total abundance
1	Aculeata sp.1	2	8	10
2	Anobidae sp.1	0	1	1
3	Aphididae sp.1	20	5	25
4	Apicryta sp.1	2	9	11
5	Apis mellifera	518	95	613
6	Arachnid	12	15	27
7	Bee sp.1	4	3	7
8	Bee sp.2	10	0	10
9	Bee sp.3	5	5	10
10	Bee sp.4	3	0	3
11	Braconidae sp.1	11	1	12
12	Buprestidae sp.1	0	1	1
13	Calliphoridae sp.1	14	1	15
14	Calliphoridae sp.2	24	7	31
15	*Camponotus cf nireosetosis*	6	38	44
16	*Camponotus mayri*	0	13	13
17	*Camponotus sp.11*	53	80	133
18	*Camponotus sp.2*	12	7	19
19	*Camponotus sp.23*	0	10	10
20	*Camponotus sp.3*	0	1	1
21	*Camponotus sp.5*	2	22	24
22	Carabidae sp.1	5	0	5
23	Caterpillar	1	0	1
24	Chalcidoidea sp.1	29	12	41
25	Chalcidoidea sp.4	3	12	15
26	Chironomidae sp.1		4	4
27	Chironomidae sp.2	31	3	34
28	Chrysomelidae sp.1	10	1	11
29	Chrysomelidae sp.2	37	0	37
30	Chrysomelidae sp.3	3	0	3
31	Chrysomelidae sp.4	0	1	1
32	Chrysomelidae sp.5	1	6	5
33	Chrysomelidae Sp.6	1	0	1
34	Chrysomelidae Sp.7	3	12	15
35	Chrysomelidae sp.8	1	1	2
36	Coccinelidae sp.1	3	6	9
37	Coccinelidae sp.2	21	2	23
38	Coccinelidae Sp.3	6	0	6
39	Coccinelidae Sp.4	4	0	4
40	Coccinelidae sp.5	3	0	3
41	Coleoptera sp.1	0	4	4

42	Coleoptera sp.3	0	3	3
43	Coleoptera sp.4	0	3	3
44	*Crematogaster* sp.06 (*custanea* complex)	20	105	125
45	Cucujoidea Sp.1	1	1	2
46	Cucujoidea sp.2	5	2	7
47	Cucujoidea sp.3	0	5	5
48	Cucujoidea sp.4	7	4	11
49	Damselfly sp.1	1	0	1
50	Dermestidae sp.1	0	24	24
51	Dermestidae sp.2	0	35	35
52	Diptera sp.1	0	2	2
53	Diptera sp.2	9	1	10
54	Diptera sp.4	1	1	2
55	Diptera sp.5	0	10	10
56	Diptera sp.6	5	0	5
57	Diptera sp.7	2	0	2
58	Diptera sp.8	120	3	123
59	Dragon fly	0	7	7
60	Empididae sp.1	15	2	17
61	Evanoidea sp.1	3	0	3
62	Hemiptera sp.1	4	8	12
63	Hemiptera sp.2	0	1	1
64	Hemiptera sp.3	7	3	10
65	Hemiptera sp.4	0	2	2
66	Hemiptera sp.5	0	5	5
67	Hemiptera sp.6	1	0	1
68	Hemiptera sp.7	2	0	2
69	Hemiptera sp.8	3	3	6
70	Heterocera sp.1	2	1	3
71	Heterocera sp.2	10	4	14
72	heteropteran sp.1	1	0	1
73	Heteropteran sp.2	2	2	4
74	Hetrodinae sp.1	1	0	1
75	Hydrophiloidea sp.1	0	1	1
76	Ichneumonidae sp.1	2	0	2
77	*Lepisiota crinita*	0	13	13
78	*Lepisiota sp.1* (*Capensis* gp.)	62	28	90
79	Mordelidae sp.1	1	1	2
80	Mouchera sp.1	1	0	1
81	*Musca domestica*	89	27	116
82	Mycitophilidae sp.1	2	0	2
83	Nitidulidae sp.1	12	0	12
84	Nitidulidae sp.2	5	6	11
85	Nitidulidae sp.3	0	3	3

86	Nitidulidae sp.4	2	0	2
87	Nitidulidae sp.5	1	0	1
88	Othorptera	1	0	1
89	Pentatomidae sp.1	1	1	2
90	*Pheidole* sp.1 (*megacephala*)	42	120	162
91	*Pheidole* sp.3 (*megacephala*)	52	130	182
92	*Plagiolepis* sp.1	4	4	8
93	*Polyrhachis schistacea*	21	326	347
94	Psylidae sp.1	1	3	4
95	Pyridae sp.1	0	4	4
96	Pyrrhocoridae sp.1	2	2	4
97	Reduviidae sp.1	6	5	11
98	Rhipiphoridae sp.1	0	3	3
99	Rhopalocera sp.1	3	10	13
100	Rhopalocera sp.10	0	1	1
101	Rhopalocera sp.2	8	6	14
102	Rhopalocera sp.3	0	4	4
103	Rhopalocera sp.4	2	8	10
104	Rhopalocera sp.5	0	8	8
105	Rhopalocera sp.6	9	18	27
106	Rhopalocera sp.7	1	2	3
107	Rhopalocera sp.8	0	1	1
108	Rhopalocera sp.9	1	0	1
109	Scythrididae sp.1	1	0	1
110	Syriphidae sp.1	122	15	137
111	Syriphidae sp.2	57	2	59
112	syriphidae sp.3	7	13	20
113	Tephritidae sp.1	54	2	56
114	Tephritidae sp.2	2	0	2
115	Wasp sp.1	0	1	1
116	Wasp sp.2	1	9	10
117	Wasp sp.3	2	2	4
118	Wasp sp.4	1	1	2
119	Wasp sp.5	5	9	14
120	Wasp sp.6	0	2	2
121	wasp sp.7	4	0	4
122	Wasp sp.8	1	0	1
123	Wasp sp.9	0	1	1

Appendix C A list of ant species

Ant species	Mango orchard	Natural vegetation	Total abundance
Dorylinae			
Aenictus rotundatus	126	0	126
Dolichoderinae			
Tapinoma lutenum	0	9	9
Technomyrmex pallipes	14	80	94
Ponerinae			
Anochectus traegordhi	0	2	2
Bothroponera sp.02	4	15	19
Bothroponera sp.03	0	1	1
Bothroponera strigulosa	0	21	21
Mesoponera caffraria	1	3	4
Odontomachus troglodytes	3	4	7
Ophthalmopone sp.01	2	0	2
Platythyrea lamellosa	5	48	53
Platythyrea shultzei	0	6	6
Formicinae			
Anoplolepis cf. custodiens	5	185	190
Camponotus mayri	0	1	1
Camponotus sp.02 (*rufoglaucus gp*)	2	26	28
Camponotus sp.11 (*cintellus* gp.)	10	15	25
Camponotus sp.12 (*cintellus* gp.)	3	6	9
Camponotus sp.18 (*maculatus* gp.)	4	22	26
Lepisiota crinita	67	56	123
Lepisiota sp.01 (*capensis* gp.)	111	57	168
Lepisiota sp.02 (*spinosior*.gp.)	3	1	4
Lepisiota sp.08 (*capensis* gp.)	26	20	46
Nylanderia sp.01	3	0	3
Polyrhacis schistacea	1	11	12
Tapinolepis sp.01	0	13	13
Tapinolepis sp.02	5	8	13
Myrmicinae			
Cardiocondyla sp.01	19	0	19
Carebara sp.01	0	50	50
Crematogaster sp.01 (*sub genus Sphaerocrema*)	0	2	2
Crematogaster sp.04 (*sub genus Sphaerocrema*)	2	4	6

Crematogaster sp.07	1	22	23
Meranoplus inermis	1	0	1
Meranoplus magretti	2	0	2
Monomorium albopilosum	0	82	82
Monomorium cf. drapenum	7	43	50
Monomorium cf. junodi	105	528	633
Monomorium damarense	50	269	319
Monomorium emeryi	0	190	190
Monomorium sp.12	10	96	106
Monomorium sp.13	0	2	2
Myrmicaria natalensis	33	20	53
Ocymyrmex fortiori	3	12	15
Pheidole sp.01 (*megacephala* gp.)	588	272	860
Pheidole sp.03 (*megacephala* gp.)	1860	596	2456
Pheidole sp.06 (*crassinoda* gp.)	34	74	108
Pheidole sp.07	32	69	101
Solenopsis sp.01	43	186	229
Solenopsis sp.02	2	154	156
Tetramorium baufra	1	15	16
Tetramorium cf. setigerum	5	3	8
Tetramorium notiale	2	0	2
Tetramorium setuliferum	0	1	1
Tetramorium sp.01 (*squaminode* gp.)	4	26	30
Tetramorium sp.05 (*sereceiventre* gp.)	1	40	41
Tetramorium sp.16 (*sereiceventre* gp.)	8	54	62
Tetramorium sp.18 (*simillimun* gp.)	0	1	1
Tetramorium sp.19 (*simillimun* gp.)	1	3	4
Tetramorium sp.23 (*sereiceventre* gp.)	0	11	11
Ponerinae			
Anochectus traegordhi	0	2	2
Bothroponera sp.02	4	15	19
Bothroponera sp.03	0	1	1
Bothroponera strigulosa	0	21	21
Mesoponera caffraria	1	3	4
Odontomachus troglodytes	3	4	7
Ophthalmopone sp.01	2	0	2
Platythyrea lamellosa	5	48	53
Platythyrea shultzei	0	6	6
Pseudomyrmecinae			

Tetraponera sp.01

0 1