Composition, Spatial Heterogeneity and Seasonal Turnover of Plant-Pollinator Communities in an Agriculture-Forest-Mosaic

Dissertation

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Asiyeuliza, hanalo ajifunzalo.

He, who does not ask questions, has nothing to learn.
Swahili saying

CONTENTS

10. Acknowledgements

11. Curriculum Vitae

1. SUMMARY

Agricultural land currently occupies approximately 38% of the planet's land surface, or around half its habitable area, and is the largest cause of native habitat loss and fragmentation. Perhaps one of the most important impacts of destruction of natural habitat is the loss of natural ecosystem services like pollination, through reduction in species richness and abundance of pollinator guilds, and the resulting reduction in the reproductive success of plants relying on pollination by these animals. As bees have rather small foraging ranges (solitary bees: 150m – 600m, African honeybees: 400m - 1000m), local habitat structure and resource configuration appear of great importance to their behaviour and survival. As pairs of pollinator and plant species do not interact in an ecological vacuum, we need more than the analysis of pairwise interactions to understand the evolution of diversified mutualisms, and their role in the ecosystems. Community-wide approaches, like food webs, are a fundamental component of any attempt to describe how natural communities are structured.

To assess the impact of habitat conversion on biodiversity and ecosystem processes I investigated (i) the composition and spatial as well as temporal heterogeneity of plant-flower visitor networks, (ii) the flower visitor community together with its pollination service for the herbal plant *Justicia flava* (Acanthaceae) and (iii) the spatial heterogeneity of *J. flava*'s flower visitors in an agriculture-forest mosaic. These studies were conducted in and around the Kakamega Forest, a tropical rain forest remnant and its surrounding structurally diverse agricultural area in Western Kenya.

The flower visitor networks in the three different habitat types farmland, forest edge and forest interior differed highly in size, with the bigger networks in the agricultural and thus open and disturbed areas. The flower visitor webs in all three habitat types were highly asymmetric, with the three most involved plant species building 54% – 84% of the network. *Apis mellifera* was the most abundant bee species in all habitats, and was involved in 60% - 80% of the interactions in the networks. Species turnover was very high between habitat types, indicating connectivity as well as interplay between the different habitats. Seasonal turnover was found to be high only inside the forest, the habitat with the highest fluctuation in flower and thus food availability. The floral resources were found to be the best explaining factor rather than other habitat parameters for network size in this structurally rich and diverse landscape.

Focusing on the common herbal plant *Justicia flava* (Acanthaceae), I found 74 species of insects visiting the flowers, with only 2-19 species per study site. While highest species richness was found in the farmland, highest diversity (both species richness and eveness) was found inside the forest. Due to a high dominance of honeybees, the abundance of flower visitors outside the forest was extremely high. Up to a distance of 1500m from the forest, the number of bee species visiting the flowers of *Justicia flava* decreased significantly with increasing distance from the forest whereas the flower visitor composition on study sites farther from the forest did not show any dependency on the distance. The reproductive success of the self-incompatible plant was neither influenced by the diversity nor by the abundance of flower visitors, due to the fact, that *J. flava* seemed to be a keystone food source for several bee species and thus experienced high visitation frequencies. Hence, the plants' reproductive success was not pollinator-limited, but rather resource-limited (water-limited) due to a very dry observation season. Even if diversity and abundance of pollinators did not show any direct influence on fruit and seed set of *Justicia flava* in this rather short-term observation, the composition of the visitor communities are of great importance for the long term preservation of the plant's reproductive success and thus the maintenance of the plant pollinator system.

Comparative results showed, that the composition of flower visitors of *Justicia flava* was spatially heterogeneous not only between different habitats, but also between study sites closely located in the same habitat type (distance between 200m – 2000m). Especially inside the forest, spatial autocorrelation in flower visitor composition was found, with flower visitor communities in close vicinity to each other being more similar compared to compositions farther apart. This pattern might be due to different foraging regimes in the different habitat types, with random foraging in the flower-rich open areas compared to a more traplining-behaviour inside the flower-poor forest. Furthermore, the results showed, that bee species compositions in forested areas with small numbers of flowers were spatially heterogeneous and thus difficult to predict. As geographic differences in interactions are an inherent part of the coevolutionary process, and geographically structured species tend to coevolve towards a complex spatial mosaic of coevolutionary hot spots and cold spots, there is the potential of coevolutionary shifts in the pollination system of *Justicia flava.*

To conclude, the diverse agricultural land, rather than the natural forest, acted as a stable pollinator reservoir due to its large floral resources. Hence, the conservation of the whole countryside, not only the forest, is important to preserve the ecosystem service pollination for natural plants as well as crop plants in Kakamega area.

2. GENERAL INTRODUCTION

2.1 Tropical agriculture-forest mosaics: changes in landuse patterns and biodiversity

Global biodiversity is changing at an unprecedented rate (PIMM ET AL. 1995) as a complex response to several human-induced changes in the environment (VITOUSEK 1994), like land use change, habitat fragmentation and climate change. The magnitude of biodiversity change is so large (PIMM ET AL. 1995) and so strongly linked to ecosystem processes (CHAPIN ET AL. 1997, LUNDBERG & MOBERG 2003) and society's use of natural resources (DAILY 1997, COSTANZA ET AL. 1997) that biodiversity change is considered an important global change in its own right nowadays (WALKER & STEFFEN 1996, SALA ET AL. 2000). Estimates of complete habitat conversion vary by biome from 0.4% (tundra) to 48.5% (tropical/subtropical dry broadleaf forests), but a much larger area is directly influenced by human activities to some degree (SANDERSON ET AL. 2002, HOEKSTRA ET AL. 2005). Agricultural land currently occupies approximately 38% of the planet's land surface, or around half its habitable area (DONALD & EVANS 2006), and is the largest cause of native habitat loss and fragmentation (DEFRIES ET AL. 2004, WILLIAMS & KREMEN 2007), followed by climate change, nitrogen deposition, biotic exchange and elevated carbon dioxide concentration (SALA ET AL. 2000). In the developing world, the area of agriculture (particularly in South America and sub Saharan Africa) may increase by more than 30% by 2050 (TILMAN ET AL. 2001), occupying a new area approximately equal to that of all the planet's remaining rainforests (MAYAUX ET AL. 1998). The conversion of native forests to croplands and the increasing agricultural intensification have led to simplification of landscape structure, furthermore to declines in diversity and abundance of many taxa of animals and plants (MYERS 1992, SALA ET AL. 2000, BENTON ET AL. 2002, TSCHARNTKE ET AL. 2005) and consequently to species extinctions.

While large-scale commercial logging operations are major drivers of deforestation in South America and Asia, the pattern in sub-Saharan Africa is different. Here, countries holding tropical rainforests are characterized by highest population densities and growth rates.

As people show very low per capita income, they rely on subsistence farming and the utilization of forest products, like fuelwood and bush meat. One result of these population densities and the related smallholder agriculture is a highly structured and diverse agricultural land, a complex landscape mosaic. CARROLL ET AL. (2004) highlighted, that the negative effects of habitat-isolation on species diversity and abundance and thus on the functioning of ecological processes, are reduced as the quality of the matrix increases. Thus, smallholder agriculture is often important for the maintenance of biodiversity (RICKETTS ET AL. 2001, KLEIN ET AL. 2006) and can provide habitat for a variety of organisms normally associated with forest (THIOLLAY 1995, PERFECTO & VANDERMEER 2002). Consequently, this smallholder agriculture could be an important component of landscape- or regional-level conservation strategies, especially in sub-Saharan Africa, where population growth, deforestation and rural poverty are acute problems (WORLD BANK 2001) with strong "positive" influences on annual rates of deforestation and landuse change (LAURANCE 1999).

However, in Africa, most scientific work is still focusing on the natural landscapes, disregarding the high importance of such well structured smallholder agricultural areas. Especially in Europe and North America, scientists are aware of the importance of the farmland respectively the complete countryside (DAILY ET AL. 2001, STEFFAN-DEWENTER ET AL. 2002, LUCK & DAILY 2003, HOLZSCHUH ET AL. 2007) for the maintenance of biodiversity (e.g. KLEIJN ET AL. 2006) and attention is given to the functioning of landscape mosaics.

2.2 The ecosystem service pollination and habitat conversion/fragmentation

Perhaps the most important impact of destruction of natural habitat, and especially of tropical forests, is the loss of natural ecosystem services. Ecosystem services are all the natural services provided by ecosystems that are useful to humans (DAILY 1997, LOREAU ET AL. 2002, LUCK & DAILY 2003, KREMEN 2005, KLEIN ET AL. 2006), such as soil nutrient supply, soil carbon storage and biodiversity-related services like pollination, seed dispersal, decomposition, natural control of pests and invasive species. Some ecosystem services, such as pollination and seed dispersal, are produced at a local scale by mobile organisms foraging within or between habitats (LUNDBERG & MOBERG 2003, SEKERCIOGLU 2006). Although these mobile organisms deliver services locally, their individual behaviour, population biology and community dynamics are often affected by the spatial distribution of resources at a variety of spatial (and also temporal) scales from local (single patch) to landscape (e.g. composition and connectivity of habitats) (LEVIN 1992, MCGARIGAL & CUSHMAN 2002, WILLIAMS & KREMEN 2007).

To understand how changes in landscape composition affect pollination processes and other species interactions, knowledge about the responses of the mobile species to habitat parameters and their changes are essential. Studies from throughout the world indicate that landscape fragmentation and degradation often lead to declines in diversity and abundance of insect pollinators as well as the interacting plant species (AIZEN & FEINSINGER 1994, CUNNINGHAM 2000, AIZEN ET AL. 2002, KLEIN ET AL. 2002, RICKETTS 2004). However, a few studies found positive effects of habitat fragmentation and forest loss on diversity and abundance of bees, though (TAKI ET AL. 2007, WILLIAMS & KREMEN 2007). Furthermore, some researchers have suggested that bees may be buffered to the effects of fragmentation (CANE 2001), as they inherently rely on patches of resources that are commonly separated from nesting sites (OSBORNE ET AL. 1999, MORRIS ET AL. 2001, WILLIAMS AND TEPEDINO 2003) rather than on continuous more or less monotonous habitats. Populations of many species exist at the interface of agricultural and natural areas or within agricultural landscapes, using the whole habitat mosaic. Landscape level factors, such as the amount and distribution of various habitat types, the resources they contain, and the connectivity among habitat types, are critical to maintaining bee populations (KREMEN ET AL. 2002, STEFFAN-DEWENTER ET AL. 2002, WILLIAMS & KREMEN 2007). The rate, timing, duration, frequency, and spatial extent of the mobile links could all be affected by changes in landscape composition (DUKES & MOONEY 1999, HARRINGTON ET AL. 1999, HUGHES 2000), leading to profound changes in local ecosystems (POST ET AL. 1998). Especially the connectivity among habitats will likely be crucial for persistence of pollinator populations as natural habitats are increasingly fragmented by human activities. Recent studies showed that connectivity was critical for offspring as increasing isolation from natural habitat decreased offspring production and survival for bees (WILLIAMS & KREMEN 2007). All these different findings highlight the complexity of the topic as well as the need for greater attention to how populations and communities perform in different habitats and at their interface.

Bees move actively between habitats and ecosystems and are thus essential components in the dynamics of ecosystem development and ecosystem resilience (that is buffer capacity and opportunity for reorganization) that provides ecological memory (that is, sources for reorganization after disturbance) (MOBERG & FOLKE 1999). They help to sustain the capacity of ecosystems to supply the ecological services essential for social welfare and economic development (COSTANZA ET AL. 1997, CHAPIN ET AL. 2000). In this sense, they often provide functions analogously to keystone species (PAINE 1969).

2.3 Human dependence on the ecosystem service pollination

Pollination is not only mutually beneficial to the interacting plants and animals, but also serves humanity directly through the yield of many crops, and indirectly by contributing to the healthy functioning of unmanaged terrestrial ecosystems (COSTANZA ET AL. 1997, NABHAN & BUCHMANN 1997, KLEIN ET AL. 2007).

One-third of the world's crops demand pollination to set seeds and fruits (e.g. BUCHMANN & NABHAN 1996, KLEIN ET AL. 2007) and the great majority of them are pollinated by many of the estimated 25,000 species of bees (ROUBIK 1995). The estimated annual value of this service worldwide is US$ 65-70 billion (PIMENTEL ET AL. 1997). The most widely used species in crop pollination is the honeybee (*Apis mellifera*), which in many parts of the world has contracted serious diseases resulting in decreasing numbers of colonies. A major problem is emerging for the world's agricultural production, reflecting the risk involved in relying on a single pollinator species (BUCHMANN & NABHAN 1996). As many species of native bees are known to be efficient pollinators of crops and a few species have been managed for this purpose, farmers nowadays are interested to use the service of native bees. However, the numbers of native bees are dwindling. Declines in numbers have been reported in North and Central America (e.g. ALLEN-WARDELL ET AL. 1998) and Europe (OSBORNE ET AL. 1991, BANASZAK 1996, BIESMEIJER ET AL. 2006). The losses are due to mostly the use of agrochemicals, to land use changes like deforestation and monocultures and possibly to the introduction of exotic pollinators as well (e.g. HINGSTON & MCQUILLAN1999, GOULSON 2003, INARI ET AL. 2005, INGS ET AL. 2006).

The so called 'pollinator crisis' exemplifies the intimate relationship existing between the welfare of natural environments and their biodiversity and the needs of sustainable agriculture. On the basis of the convention of biodiversity (Rio de Janeiro 1992), the International Pollinators Initiative was started, to emphasize the importance as well as vulnerability of the ecosystem service pollination and to investigate especially in understanding and conserving the dynamics and patterns of pollination interactions.

2.4 Plant-pollinator networks

Pollination of flowers is an essential step in the sexual reproduction of angiosperms. Most angiosperm species rely on insects or other animals (90% of the estimated 240.000 flowering plant species, NABHAN & BUCHMANN 1997), rather than wind, for transfer of pollen among individual plants. It has even been suggested that the reproductive success of plants is often more limited by pollinator scarcity than resource scarcity (BURD 1994). The pollinators in turn benefit by obtaining floral resources such as nectar or pollen.

As pairs of pollinator and plant species do not interact in an ecological vacuum, we need more than the analysis of pairwise interactions to understand the evolution of diversified mutualisms such as animal-mediated pollination, and the outcomes of their interactions are best viewed within the network of community-level interactions. All individuals and species are linked in networks through interactions like predation, parasitism or pollination. Community wide approaches, like food webs, are a fundamental component of any attempt to describe how natural communities are structured, how complexes of species interact (LAWTON 1995, MEMMOTT 1999), how mutualisms evolve (JORDANO 1987, MEMMOT 1999, BASCOMPTE 2007) and how pollinators can be managed in crop situations (ALLEN-WARDELL ET AL. 1998). In nature, networks of species interactions are ‘the architecture of biodiversity’ (JORDANO ET AL. 2006), because community dynamics rely deeply on the way species interact. Most pollination interactions are not specific and do not involve tight mutualisms between species pairs, yet pollination interactions are paradigmatic examples of coevolved interactions among animals and plants.

2.5 The study area: Kakamega Forest and its surrounding farmland

The studies were conducted in and around the Kakamega Forest (Figure 2.1), a tropical rain forest remnant and its surrounding agricultural areas. The forest is located in western Kenya (0°17’N, 34°54’E) at an altitude of 1500 m to 1700 m, about 50 km north of Lake Victoria. The annual rainfall reaches about 2000 mm, and is more or less well distributed over the year, with two distinct rainfall peaks. The mean monthly temperatures range from 11°C to 29°C, with an average temperature of 22°C. The Kakamega Forest is considered to be the easternmost remnant of the lowland guineo-congolian rain forest belt (KOKWARO 1988) with rain forest dwelling animals and plants. Furthermore, due to its elevation it also contains montane elements of flora and fauna (ALTHOF 2005). Kakamega Forest is severely overexploited due to its small size and dense surrounding human population. The forest’s area covers an estimated 12000 ha (BENNUN & NJOROGE 1999, LUNG & SCHAAB 2004). Apart from the main forest area there are 5 isolated forest fragments situated around the forest (BROOKS ET AL. 1999). About 4000 ha of the northern Buyangu part of the forest and the northern fragment Kisere are declared as National Reserves under management of the Kenya Wildlife Service (KWS) with conservation of biodiversity as their main dogma since 1982 (KIFCON 1994, MITCHELL 2004). This part of the forest is characterized by a series of abandoned secondary forests at different stages, including premature and mature forests. The history of the forest is well documented (Mitchell 2004). Some parts of the forest were grasslands in former times; some have been afforestated 100 years ago. In Buyangu Hill forest, logging is reported to have taken place until the 1970s.

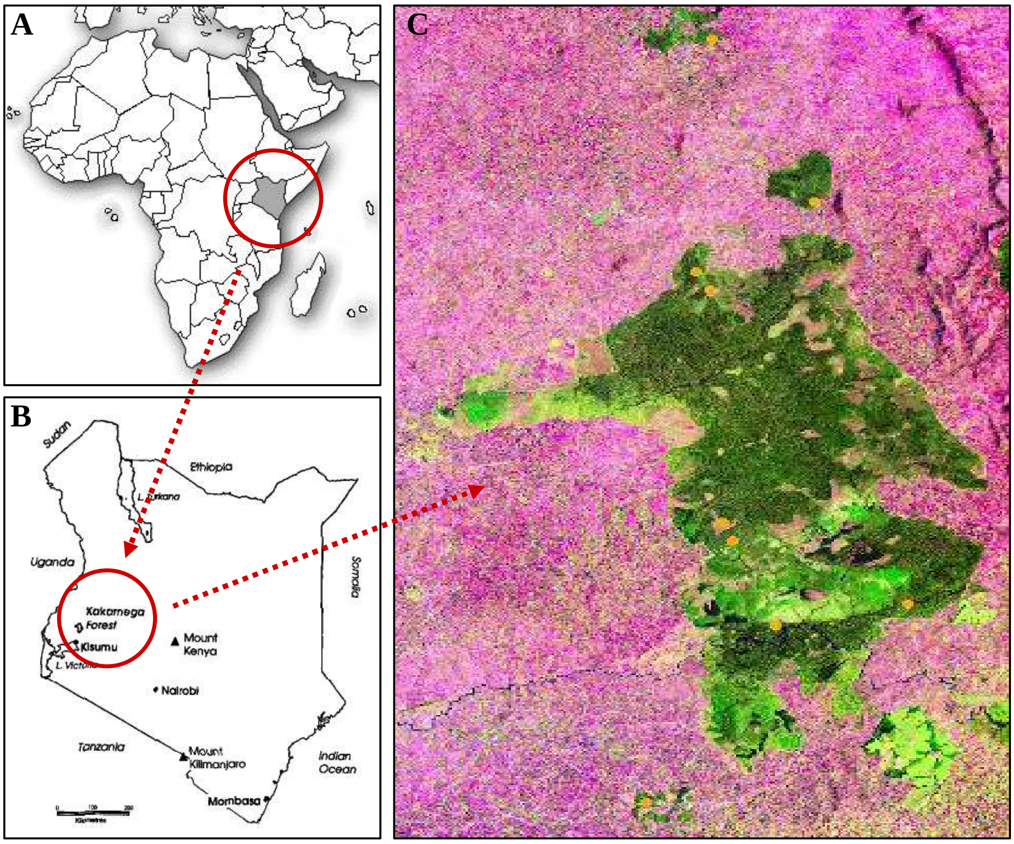

Figure 2.1:
(A) Map of Africa indicating location of Kenya; (B) Map of Kenya indicating location of Kakamega Forest; (C) Satellite image of Kakamega Forest and the surrounding farmland (Landsat ETM + (7); 05 Feb 2001, spectral bands 5/4/3, contrast enhanced; courtesy of G. Schaab)

The farmland, which borders the forest mostly without any buffer zone (Figure 2.2), has rich agricultural soils, which in combination with the temperatures makes it very suitable for farming. Jaetzold & Schmidt (1982) classified the region as one of the high potential areas in Kenya for agricultural production. The traditional small-scale farming subdivides the agricultural matrix in small land units ranging from 0.2 ha to 0.7 ha per household (Greiner 1991, MOA 2006). These small land units generate a highly structured and diverse landscape mosaic with a high proportion of diverse hedgerows, field margins, gardens, homesteads, etc.

Figure 2.2:
The farmland borders Kakamega Forest directly, without any buffer zone.

The area is one of the most highly populated rural areas in the world, with population ranging from 433 to 713 inhabitants per km^2 (Mitchell 2004), boosted by a growth rate of 2.8% a year (CINCOTTA 2000). Thus the anthropogenic impact on the forest will even be amplified and the conflict between nature conservation and land use will increase at the same time (BALMFORD ET AL. 2001). 62% of all households generate their incomes from agriculture and the district's poverty rate is about 52% (DOSE 2007). With 76% of the district's area being under agricultural cultivation and an additional 11% being covered with (gazetted) forest, an extension of cultivated areas would result in (1) an increasing monotony of the agricultural landscape, or (2) in reduction of the forest cover.

The highly structured pattern of landscape, which is under increasing pressure by the population growth, makes Kakamega Forest a suitable and interesting study area, to investigate the influence of different landscape parameters (like habitat type, food availability) on plant-flower visitor interactions. Especially the interactions in the interface between natural forest and highly structured farmland are of great concern, as previous studies usually focused on rather monotonous farmland.

In this thesis, I investigated the strength of the interplay between the different habitat types. Furthermore, the spatial and temporal patterns of pollination interactions between whole communities as well as between populations of a single plant species and its visitors were investigated. I examined, if the mutualistic interaction partners were more influenced by habitat diversity, habitat nativeness or resource availability (like soil quality, flower supply).
The thesis is divided into three major studies.

In the second chapter, the flower visitor network composition in the Kakamega Forest, the forest edge and the adjacent farmland is analysed. Specifically it was investigated to what extent the network composition differed between habitat types and seasons. The spatial and temporal turnover rates were calculated to analyse the connectedness as well as the interchange between habitats and seasons.

In the third chapter, the flower visitor composition of *J. flava* is investigated, and the influence of diversity and abundance of bees on the reproductive success evaluated. Specifically it was tested, if the flower supply, climatic factors or the distance to forest influenced the composition (diversity and abundance) of the flower visiting bees. Furthermore we tested the influence of the composition of bees, the soil conditions, and the canopy cover on the reproductive success of *J. flava*.

In the fourth chapter, the spatial composition and autocorrelation of the flower visitors of *Justicia flava* (Acanthaceae) is analyzed. Specifically it was tested, if the flower visitor communities of the herbal plant *Justicia flava* differed in composition, not only between habitats but between study sites of the same habitat. Furthermore, the spatial patterns of flower visitors were compared, and the underlying factors investigated.

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3. SPATIO-TEMPORAL VARIATION IN FLOWER VISITOR NETWORKS

3.1 Abstract

Local habitat structure and resource configuration as well as matrix structure appear of great importance to the behaviour and survival of bees. I examined the contribution of three different habitat types (farmland, forest edge, forest interior) to regional diversity in the tropics, and established the differences and overlap in plant-bee community interactions between the nearby habitats. I identified the key species in the three different webs and used network properties, like connectance, nestedness and quantified network to describe temporal and spatial variation.

The study was carried out on 18 study sites (six in each habitat type) in the Kakamega Forest area in Kenya. In total I found a number of 121 bee and 89 plant species involved in the interactions. Bees were limited by floral resources rather than other habitat parameters. Thus, highest diversity and abundance were found in the flower rich areas outside the forest. The flower visitor webs in all three habitat types were highly asymmetric, with the three most involved plant species building 54.0% - 84.0% of the network. *Apis mellifera* was the most abundant bee species in all habitats, and was involved in 60.0% - 80.0% of the interactions in the networks.

Overall, at the level of sampling conducted, α-diversity comprised 6.5% of the total diversity of the study region (121 bee species). Temporal and spatial turnover comprised 11.6% and 35.2% respectively of total diversity and the remaining 46.7% represented turnover in species between the different habitat types. Due to high similarities in bee population between the habitats as well as high seasonal fluctuations in flower abundance inside the forest, the conservation of the whole countryside is important to preserve the ecosystem service pollination for natural plants as well as crop plants.

3.2 Introduction

Modification of landscapes, like habitat fragmentation, conversion of natural habitats to agricultural areas, and intensification of agriculture can lead to changes in species diversity and composition, interruption of movements between populations and might possibly result in a reduction of gene flow as well. Some studies have shown that increased agricultural management intensity leads to decreased diversity of a variety of pollinator taxa (STEFFAN-DEWENTER ET AL. 2002, MAS & DIETSCH 2003), whereas others have demonstrated higher species richness in disturbed habitats (LAWTON ET AL. 1998, DEVRIES & WALLA 2001, KLEIN ET AL. 2002). Such divergent information shows how little is known, despite the ecological and economic importance of bees, about the drivers of bee diversity and abundance, especially in changing landscapes. However, the worldwide decline of pollinators and its consequences on ecological processes is in the focus of several scientists and subject to discussions (see GHAZOUL 2005(A), (B), STEFFAN-DEWENTER ET AL. 2005) and, in Europe, declines in pollinators and plants could be attributed to anthropogenically induced changes in habitats and climates (BIESMEIJER ET AL. 2006). But it is still not yet clear, how habitat modification affects the interactions among species. Plant-animal interactions have a pervasive influence in community dynamics and diversity, where they play a central role in the reproduction of the plants and the life histories of the animals.

Community wide approaches are a fundamental component of any attempt to describe how natural communities are structured, how complexes of species interact (MEMMOTT 1999), how mutualisms evolve (JORDANO 1987, MEMMOT 1999, BASCOMPTE 2007) and how to choose and manage pollinators in crop situations (ALLEN-WARDELL ET AL. 1998). In contrast to the complex food webs examined so far (e.g. BERSIER ET AL. 1999, WILLIAMS ET AL. 2002), plant-animal mutualistic networks embed not only the trophic relationships among mutualistic partners (JORDANO 1987), but also the complexities of the evolutionary effects on each other that drive coevolutionary processes (THOMPSON 1999). This process is rather diffuse, involving sets of generalistic as well as specialised species, and pairwise coevolution (JANZEN 1980) is very rare in most plant-animal mutualisms (THOMPSON 1982, HOWE 1984).

Pollination webs or networks are highly asymmetrically organized, with the core set of generalist species interacting with one another and the most specialized species interacting with the most generalist species only (VÁZQUEZ & AIZEN 2004). This nestedness has been shown to increase network robustness, as nested networks appear less prone to the detrimental effects of habitat loss (FORTUNA & BASCOMPTE 2006) and species extinctions (MEMMOTT ET AL. 2004). While a network would not be affected much by the disappearance of specialised interaction partners, it would react sensitively to losing generalist pollinators. These losses are predicted to be unlikely because the broad floral preferences of generalist pollinators buffer them against extinction (FORTUNA & BASCOMPTE 2006, PEMBERTON & WHEELER 2006). However, PAUW (2007) highlighted, that in a worst-case scenario, the decline of generalist pollinators is predicted to trigger cascades of linked declines among the multiple specialist plant species to which they are linked. This can lead to the acceleration of biodiversity loss (GILBERT 1978, COX ET AL. 1991). We still have a limited understanding of the consequences of network patterns for ecosystem stability and evolution (JORDANO ET AL. 2003) although the importance of conserving these interactions and associated processes has been stressed repeatedly (e.g. PAUW 2007), particularly as humans rely on ecosystem services associated with species interactions, such as pollination and biological control. Plant-pollinator communities are subject to continuous spatial and temporal changes in species composition, which is likely to influence inherent network structure. Environmental conditions and the availability of food change spatially as well as temporally throughout a species distribution range (NIELSEN ET AL. 2007) or throughout seasons (WOLDA 1988, TYLIANAKIS ET AL. 2005). Thus, it is important not to assume all partners to coexist, but to investigate the network patterns for the different seasons and habitats separately (MEDAN ET AL. 2006).

Especially in the tropics, initial studies and conservation efforts understandably focused on natural ecosystems and, more recently, on their remaining fragments (DAILY 2001). It has become clear that reserves are too few, small, isolated, and subject to change, to sustain on their own more than a tiny fraction of biodiversity and ecosystem services over the long run (BROSI ET AL. 2007). Thus, it is highly important to understand the plant-pollinator network patterns in compound landscapes or ‘countrysides’. Researchers became aware, that many countryside habitats are actually not as inhospitable as was thought before. For instance, more than half of Costa Rica’s native bird species occur in largely deforested countryside habitats, together with similar fractions of mammals and butterflies (DAILY 2001). Europe, much of which has been “countryside” for a long time, shows clearly that some farming landscapes retain more biodiversity and valuable ecosystem services than others (TSCHARNTKE ET AL. 2002, HOLZSCHUH ET AL. 2007). In the tropics, more data is highly needed as understanding how bees and their plants deal with such landscapes is increasingly important for the conservation of biodiversity as well as the ecosystem service pollination, as even small variations in the number of species can have severe effects on pollination rates.

I did the investigations in a highly structured, diverse forest-farmland mosaic in Western Kenya, where the endangered forest borders the highly populated and structured farmland. I conducted the study in three different habitat types (farmland, forest edge, forest interior), which were in close vicinity to each other. My aim was, to investigate the differences as well as similarities in composition between the three plant-pollinator webs and to highlight the unity, coherence and similarity between them. Furthermore, I was interested, which of the networks showed the highest generalization pattern. Special focus was set on spatial and seasonal fluctuations and turnover rates, and thus the variability in the composition of the flower visitor webs.

3.3 Material and methods

3.3.1 Study time and area

The study was conducted on 18 study sites located inside and around the northern part of Kakamega Forest, six in each of the three habitat types, farmland, forest edge and forest interior (Figure 3.1). Data were collected between June 2005 and July 2006 on a monthly basis in each study site.

The study sites were ten by ten meters square, and not farther than 2800m from each other, while the farthest distance between study sites of different habitats was 4500m between Kabrasi B in the farmland and Salazar B inside the forest. As, depending on the bee species, flight distances can reach up to several kilometres (JANZEN 1971, WASER 1982, ROUBIK & ALUJA 1983, CRESSWELL ET AL. 2000), bees are theoretically able to move between the chosen study sites.

Seasons

As the rainfall in Kakamega area shows a bimodal pattern, the year is subdivided into four seasons. The annual rainfall reaches about 2000 mm. The highest amount of rain is received between March – May (long rain season), while the rains between September – November are not as heavy (short rain season). Between June – August the climate is cold and dry (cold dry season) while the temperatures increase explicitly between December – February (dry season). I treated the four seasons separately in the analysis, because a full year exceeds the period of pollination activity of the average plant and animal mutualists in this system and thus e.g. overall connectance would have been seriously misleading if calculated for the whole year.

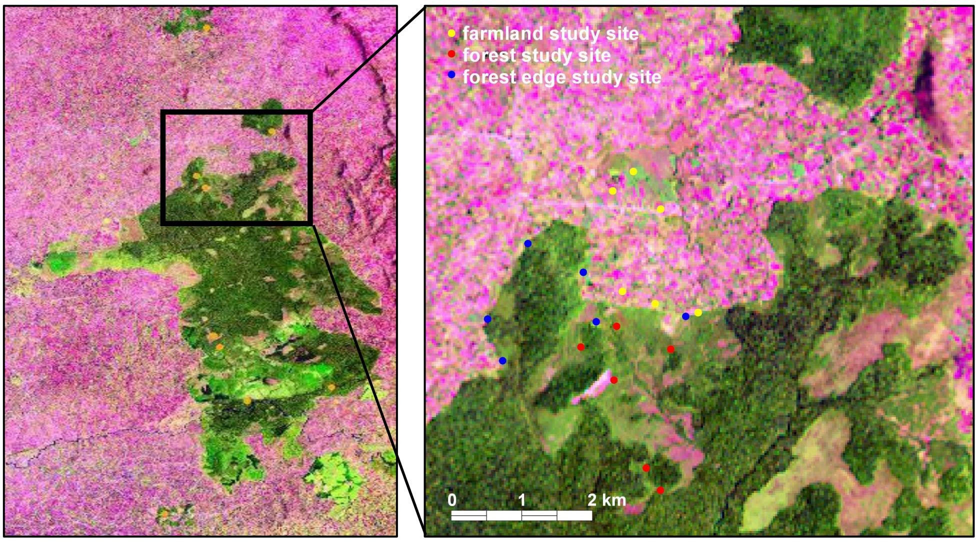


Figure 3.1:
(A) Satellite image of Kakamega Forest and the surrounding farmland (Landsat ETM + (7); 05 Feb 2001, spectral bands 5/4/3, contrast enhanced);
(B) Detail: the study area in the northern part of the forest.
courtesy of G. Schaab

3.3.2 Community structure

Plant communities

In the beginning of the study, the vegetation in the study sites was identified and mapped. The cover of canopy, giving shade to the herbal layer and thus the focal plants, was estimated using a percentage scale (from 0% = no canopy to 100% = complete canopy coverage). This canopy cover in each study site was used for analysing potential influence of the canopy cover on the visitation frequency. Parallel to the flower visitor observation units, monthly flower counts were conducted to produce a quantitative measure of flower density over time at each study site.

Flower visitor communities

Investigations on flower visiting bees were done once a month on each study site between 09.00 am and 11.00 am, and between 12.00 am and 02.00 pm, the time period with the highest insect activity and the lowest chance of interference by rain. One observation unit consisted of two 30-minutes catching periods hour after hour (09.00-09.30 plus 10.00-10.30, or 12.00-12.30 plus 13.00-13.30). Twelve observation units were conducted on each of the 18 study sites. Unknown insects were caught, well known bees only observed and listed to reduce the negative impact on the bee community. In every observation unit, every bee, the number of flowers and the identity and number of different plant species it visited, were recorded. The data on flower abundance were used as a measure for attractiveness and food availability for the flower visitors.

Diversity of flower visitors

The within-habitat-diversity of flower visitors was calculated using the Rényi diversity profiles. The use of non-parametric index families allows the diversity of a community to be characterized by a (scale-dependent) diversity profile instead of a numerical value (TÓTHMÉRÉSZ 1998). The first of these techniques, the 'generalized entropy', was published by RÉNYI (1961).

$$H_\alpha = \frac{\ln\left(\sum_{i=1}^{s} p_i^\alpha\right)}{1-\alpha}$$

p_i = proportions of each species
α = scale parameter

A profile is calculated by changing the value of α from 0 to infinity. In this thesis, the values of α are: 0, 0.25, 0.5, 1, 2, 4, 8, 16, Infinity (Inf.).

The scale parameter α:

$\alpha = 0$ => information on species richness; the profile value is the logarithm of the species richness
$\alpha = 1$ => Shannon diversity index
$\alpha = 2$ => logarithm of the reciprocal Simpson diversity index
α = infinity => provides information on the proportion of the most abundant species. Profiles that are higher at α = infinity have a lower proportion of the dominant species.

The shape of the Rényi-curve profile is an indication of the eveness. A horizontal profile indicates that all species have the same abundance. The less horizontal a profile is, the less evenly species are distributed. If the profile for one site is everywhere above the profile for another site, then this means that the site with the highest profile is the more diverse of the two. If the profiles intersect, it is not possible to order the sites from lowest to highest diversity (KINDT & COE 2005). The Rényi Diversity profiles were produced, using R 2.4 (THE R DEVELOPMENT CORE TEAM 2006) and the R package vegan 1.8-3 (OKSANEN ET AL. 2006).

Due to the fact, that there was not a single "diversity-value" for the flower visitor communities of each site, the Rényi diversity index could not be used for further statistical analyses. Thus, the species richness was used, which was defined here as the number of species, independent of the species' abundance and the community's eveness.

Partitioning of bee species diversity across spatiotemporal scales

I partitioned biodiversity as followed: (1) α'-diversity, which is the average diversity within a plot, (2) γ-diversity, which is the total diversity across plots and (3) β-diversity, the difference between γ (total) diversity and α' (local), which is a measure of the variation of species composition between plots or seasons. I used the additive diversity partitioning method (LANDE 1996), such that $\gamma = \alpha' + \beta_s + \beta_t$. This technique is insensitive to differences in sampling effort among replicates, and therefore, rarefaction of data prior to analyses was not necessary. In this study I partitioned the β-diversity in between-site β-diversity (β_s) and between-season β-diversity (β_t) for all habitat types. The temporal turnover in species richness between seasons was calculated for each plot (β_{tplot}) within a given habitat type as the total number of species found within that plot (over the entire year) minus the mean number of species per season for that plot (α'). Overall β_t was calculated as the mean β_{tplot} for a given habitat type. Spatial turnover β_s was calculated as the total number of species found within a habitat type over the entire year minus the mean number of species per plot of that habitat type (over the entire year). As the results of Rényi-diversity profiles are equations rather than single values, I used α' in the additive diversity partitioning method, which is the number of species found in each study site.

In this study, abundance is defined as the number of individuals of a certain group, visiting flowers in the study site during the observation period.

Quantitative similarity measurements

The similarity between the different study sites was investigated using Morisita-Horn Similarity measurements (MORISITA 1959, HORN 1966). This index measures similarity between two communities and varies from 0 (no similarity) to about 1.0 (complete similarity). The index is nearly independent of sample size and compares abundances, species by species (CHAO ET AL. 2005).

$$C_H = \frac{2\sum X_{ij} X_{ik}}{\left[\left(\sum x_{ij}^2 / N_j^2\right) + \left(\sum x_{ik}^2 / N_k^2\right)\right] N_j N_k}$$

C_H = Morisita-Horn index of similarity between sample j and k
X_{ij}, X_{ik} = number of individuals of species i in sample j and sample k
$N_j = \Sigma X_{ij}$ = total number of individuals in sample j
$N_k = \Sigma X_{ik}$ = total number of individuals in sample k

3.3.3 Visitation webs

There are actually two webs to consider when working on plant-pollinator communities. First, a plant visitation web which identifies the flower choices made by putative pollinators and second, a pollinator web which quantifies pollen transfer, thus showing which insect species pollinate which plant species. I investigated the visitation webs only.

Structure of visitation webs

Following OLESEN & JORDANO (2002), I analysed different descriptive structural parameters to characterize the visitation webs of the different habitat types in the different seasons. I counted (1) the number of plant species (*P*), (2) the number of flower visiting bee species (*B*), (3) the total number of interactions recorded (*I*), (4) the total number of flower visits recorded (N), (5) I calculated the network size ($M = P \times B$) and (6) the connectance ($C = 100(I / M)$). As in year-long active systems network composition and size can fluctuate during the year, impossible interactions between partners that never overlap in time, so-called forbidden links (sensu JORDANO ET AL. 2003), can occur. Thus, C based on the overall community would overestimate the level of generalization. Therefore, I calculated the overall connectance as the average connectance of the seasonal networks, as proposed by MEDAN ET AL. (2006).

Connectance is a scale- or M-independent measure of the generalization level of a network (JORDANO 1987). In addition, I used two measures of generalization at the species level: mean number of interaction partners (= plants) across bee species ($L_{mBee} = I / B$) and mean number of interaction partners (= bees) across plant species ($L_{mPlant} = I / P$). Furthermore I determined the linkage level (= the number of interaction partners) of the most-connected animal and plant species (L_{max}). I used *Pajek software for Network Analysis* (BATAGELJI & MRVAR 1996) to analyze and draw the flower visitor networks.

Quantified visitation rate

Following the definition of KAISER ET AL. (2006), I used the following equation to analyse the quantified visitation rate, which takes into account the abundance of flowers and animals in the community, and is thus more convincing than qualitative flower visitor webs only.

$$Q_{total} = \sum_{p=1}^{n} \left(\sum_{a=1}^{m} \left(v_a \times f_p \right) \right)$$

Q_{total} = quantified visitation rate of all animal species to all plant species
v_a = total number of visits hour^{-1} flower $^{-1}$ of animal species a to plant species p
f_p = floral abundance of plant species p

Measure of nestedness

I estimated an index of matrix nestedness (N) by using *Nestedness Calculator* software (ATMAR & PATERSON 1993(a,b)). Given a particular number of plants (P), bees (B), and interactions (L), an isocline of perfect nestedness was calculated for each matrix. The unexpected presences and absences of interactions occurring in real data were weighted in a way that bounds the so called temperature T from zero (perfect nestedness) to 100 (perfect non-nestedness). The idiosyncratic temperature, the contribution of each row (plant) and column (bee) to T was calculated. Furthermore, I compared the observed T values with expected values under the assumption that presences were randomly assigned to any cell within the matrix (null model) to assess the significance of nestedness (Monte Carlo simulations, 1000 runs each). Following BASCOMPTE ET AL. (2003) I emphasized nestedness instead of disorder. Hence I calculate the nestedness N as: $N = (100 - T)/100$, with values ranging from 0 to 1 (maximum nestedness). Nestedness measures were done for the habitat types in total as well as for the different seasons in detail.

3.3.4 Data analysis and statistics

In this study the received data were listed with Microsoft Office Excel 2003. Rényi diversity profiles were produced, and Morisita-Horn Similarity calculated, using R 2.4 (THE R DEVELOPMENT CORE TEAM 2006) and the R package vegan 1.8-3 (OKSANEN ET AL. 2006). Further statistical tests were conducted using SPSS 12.0. A result was called significant, if the significance level was $p \leq 0.05$, highly significant, if the level was $p \leq 0.001$ and marginally significant, if $0.10 \geq p > 0.05$.

3.4 Results

3.4.1 Community structure

Plant communities

The total number of plant species was highly similar between the three habitats (farmland: 152 species, forest edge: 150 species, forest interior: 142 species). But differences in vegetation structure were obvious. While, tree species dominated the plant community inside the forest, herbal plants built 95% of the vegetation in the farmland. The proportion of flowering plants which were involved in interactions was rather low and differed significantly between habitats (One-way ANOVA: F(2,15) = 13.386, p < 0.001, Post hoc Tukey HSD). While about 32% of the flowering plants were involved in interactions in the farmland, this proportion was smaller at the forest edge (24%) and inside the forest (12%) (Table 3.1). The numbers of plant species involved in interactions varied between seasons. Especially inside the forest, differences were notable, with numbers of interacting plant species varying between three (in the long rain season) and 14 (in the short rain season).

Table 3.1:
Number of plant and bee species and abundance of flowers and bees in the different seasons and habitats

Habitat Type	Season	no. of plant species	no. of flowering plant species	mean no. of flowers	no. of plants in interactions	no. of bee species	no. of flower visits	no. of recorded interactions (I)	no. of solitary species	no. of flower visits by solitary bees	no. of social bee species	no. of flower visits by social bees
farmland	long rain	152	36	79	22	31	718	71	28	87	3	631
	cold dry	152	41	50	14	36	649	54	33	102	3	547
	short rain	152	51	183	15	27	323	49	24	80	3	243
	dry	152	39	49	15	31	207	47	29	71	2	136
	all seasons	152	66	90	38	67	1897	160	64	340	3	1557
forest edge	long rain	150	42	71	20	44	301	65	40	132	4	169
	cold dry	150	56	84	21	47	410	74	44	132	3	278
	short rain	150	56	199	21	37	445	65	35	108	2	337
	dry	150	37	62	10	44	231	64	42	141	2	90
	all seasons	150	85	104	37	92	1387	194	88	513	4	874
Forest	long rain	142	29	25	3	9	25	9	8	12	1	13
	cold dry	142	35	39	10	32	452	38	31	45	1	407
	short rain	142	37	45	14	20	157	29	17	38	3	119
	dry	142	35	34	4	20	66	23	19	34	1	32
	all seasons	142	60	36	18	51	700	69	48	129	3	571

As the number of flowers in a study site at a given time is a good predictor for the attractiveness of the given study site for flower visitors, I counted the number of flowering plant species and their flowers after every observation unit. Smallest numbers of flowers were found inside the forest, while highly significantly more flowers were found at the study sites in farmland and forest edge (one-way ANOVA: $F_{(2,213)} = 6.899$, $p = 0.001$; Post hoc Tukey-HSD). In the farmland and at the forest edge, the numbers of flowers varied significantly between seasons (One-way ANOVA: farmland: $F_{(3,69)} = 3.731$, $p = 0.015$; forest edge: $F_{(3,69)} = 6.34$, $p = 0.001$, Table 3.1), with the short rain season showing the highest flower abundance. Inside the forest, no differences in flower numbers were found between the seasons (One-way ANOVA: $F_{(3,69)} = 1.071$, $p = 0.367$).

Flower visitor communities

In total I found 121 species of bees on the 18 study sites in a one-year observation period, with the forest edge being the significantly most diverse habitat with 92 bee species, while in farmland and forest interior only 67 respectively 51 species were found (One-way ANOVA: $F_{(2,32)} = 5.641$, $p = 0.008$). Not only highest species richness but also highest eveness was found at the forest edge (Figure 3.2A). Bees were most abundant in the farmland (One-way ANOVA: $F_{(2,32)} = 7.275$, $p = 0.002$), due to the high proportion of social bees (especially *Apis mellifera*) in the flower visitor community. The proportion of solitary bees in the flower visitor abundance differed greatly between habitats. While the proportion was relatively low

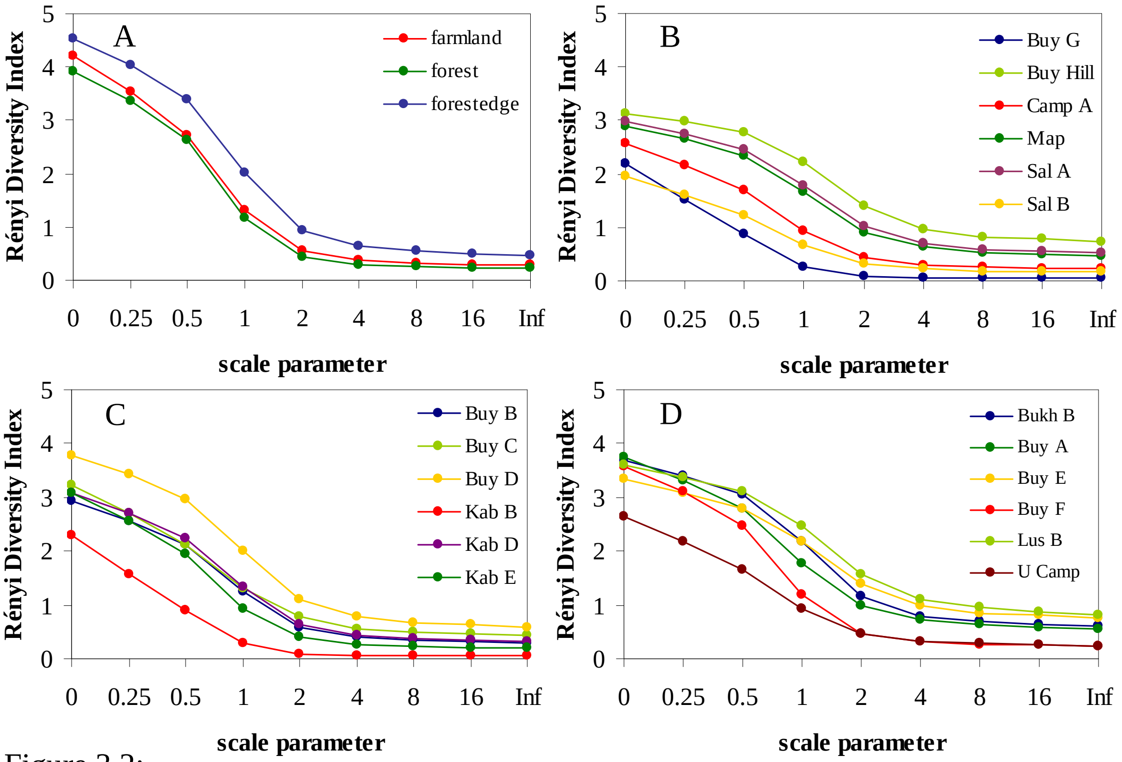


Figure 3.2:
Rényi Diversity Profiles of the bee species communities; the steeper the shape of a profile, the lower is the eveness.
(A): Profiles of all species in the different habitats; (B) For the different seasons in the farmland;
(C) For the different seasons at the forest edge; (D) For the different seasons inside the forest.

in the farmland as well as inside the forest (farmland: solitary bees: 17%, forest interior: solitary bees: 18% of all flower visits recorded), the proportion was significantly higher at the forest edge (solitary bees: 37%, One-way ANOVA: $F_{(2,16)} = 5.469$, $p = 0.016$, Post hoc Tukey HSD). Inside the forest, highly significantly bigger bee species occurred (One-way ANOVA: $F(2,719) = 11.627$, $p < 0.001$, Post hoc Dunnett).

The bee species composition did not only differ on the spatial but also on a seasonal scale. In all habitats, highest numbers of species were found in the cold dry season, while the highest eveness values occurred in the dry season (Figure 3.2 B-D). Comparisons of Rényi-profiles were difficult, due to crossings of the profiles. The highest abundance of social bees was found in different seasons depending on the habitats. In the farmland, the highest abundance was found in the long rain season, at the forest edge in the short rain season, and inside the forest in the cold dry season (Table 3.1). For detailed information on study site level see Appendix 3.1.

3.4.2 The most important plant and bee species in the webs

In all three habitat types, the herb *Justicia flava* was the plant with the highest number of flower visits (farmland: 24.8% of all flower visits, forest edge: 46.9%, forest interior: 39.3%). Furthermore, it was the most connected plant species, with 39 interaction partners in the farmland, 40 inside the forest and 59 at the forest edge (Table 2, Appendices 3.2-3.10). The other important species differed between habitats as shown in Table 2. In all habitats, the three most important plant species were involved in more than 50.0% of the observed interactions, and showed a highly generalized pattern.

The most abundant bee species was the honeybee *Apis mellifera*, which was involved in at least 60.0% of the observed interactions (farmland: 75.0%, forest edge: 61.9%, forest: 80.0%) and dominated the bee communities. It was the most connected bee species with 11 interaction partners in the forest, 12 at the forest edge and 25 in the farmland. The three most important bee species were involved in more than two-thirds of all observed interactions. While *Apis mellifera* was not only very dominant, but also visitor to a great number of plant species, some of the other dominant bee species were rather “specialized”, visiting only a few plant species, but with a high frequency (Table 3.2).

The most dominant bee and plant species were very common and rather habitat-non-specific species, and thus, found at most of the 18 study sites (*Apis mellifera* (18 sites), *Xylocopa calens* (13 sites), *Meliponula bocandei* (12 sites), and *Amegilla* aff. *langi* (11 sites)) and in all seasons.

Table 3.2:
Proportions of the most important plant and bee species in the different habitat types

	plant species	%	no. links	bee species	%	no. links
Farmland	*Justicia flava*	24.83	39	*Apis mellifera*	75.00	25
	Bidens pilosa	15.66	17	*Meliponula bocandei*	6.75	4
	Tithonia diversifolia	14.13	7	*Xylocopa calens*	2.27	2
forest edge	*Justicia flava*	46.94	59	*Apis mellifera*	61.93	20
	Cordia abyssinica	10.09	1	*Ceratina* sp.	4.10	12
	Bidens pilosa	4.11	11	*Amegilla acraensis*	1.80	2
Forest	*Justicia flava*	39.28	40	*Apis mellifera*	80.00	11
	Harungana madagascariensis	26.00	1	*Xylocopa melissa*	3.42	2
	Maesa lanceolata	19.28	1	*Meliponula bocandei*	1.14	2

3.4.3 Partitioning of bee species diversity across spatiotemporal scales

The different habitat types did not show substantial differences in the relative partitioning of diversity across space and time. In each of the three habitats, spatial species turnover was relatively high, while temporal turnover was rather low (Table 3.3). At the forest edge spatial as well as temporal species turnover were significantly higher compared to the other two habitat types (One-way ANOVA: spatial turnover: $F_{(2,17)} = 9.431$, $p = 0.002$; temporal turnover: $F_{(2, 17)} = 5.069$, $p = 0.021$), which is consistent with the larger flower visitor network at the forest edge. Correcting for the different web sizes, differences were not significant between habitats (Table 3.3). High β-diversity values indicate large differences between sites or seasons in the identity of species encountered.

Overall, at the level of sampling conducted, α-diversity comprised 6.5% of the total diversity of the study region (121 bee species). Temporal and spatial turnover comprised 11.6% and 35.2% respectively of total diversity and the remaining 46.7% represented turnover in species between the different habitat types.

Table 3.3:
Proportion of total (γ) diversity partitioned into α diversity and temporal (βt) and spatial (βs) turnover

	α	% of γ	βtplot	% of γ	βsplot	% of γ	γ
Farmland	9.00	7.20	14.67	11.73	43.33	34.67	125.00
forest edge	11.58	6.71	21.08	12.23	59.33	34.41	172.42
Forest	5.17	5.33	9.83	10.15	36.00	37.18	96.83
Total	8.58	6.53	15.19	11.56	46.22	35.17	131.42

Similarities between study sites

In comparison to the species turnover rates, which I calculated above, the Morisita Horn similarity measurements take into account not only qualitative data, but also the abundance of the flower visitors. Morisita-Horn Similarity values between the bee species compositions in the different habitats were very high (farmland – forest edge: S = 0.97, farmland – forest: S = 0.99, forest edge – forest: S = 0.96).

Taking into account the whole flower visitor community, I found the species compositions to be highly similar between the different seasons in the farmland (Table 3.4A). In the other two habitats similarity values were lower between the seasons, showing a higher degree of temporal species turnover compared to the farmland. Remarkable were the comparatively low similarity values between the cold dry and short rain season inside the forest as well as the cold dry and short rain season at the forest edge in comparison to all other seasons and habitats. The former four units were characterized by high numbers of flowers, high numbers of bee species and high numbers of interactions (Table 3.1).

Excluding the social and highly dominant bees from analysis, similarities between the units decreased significantly (farmland – forest edge: S = 0.77, farmland – forest: S = 0.43, forest edge – forest: S = 0.45, Table 3.4B), but the pattern was still the same: especially inside the forest, bee species compositions in the cold dry and short rain seasons were dissimilar compared to the other bee communities in other seasons and / or habitats.

3.4.4 Visitation webs

Structure of visitation webs

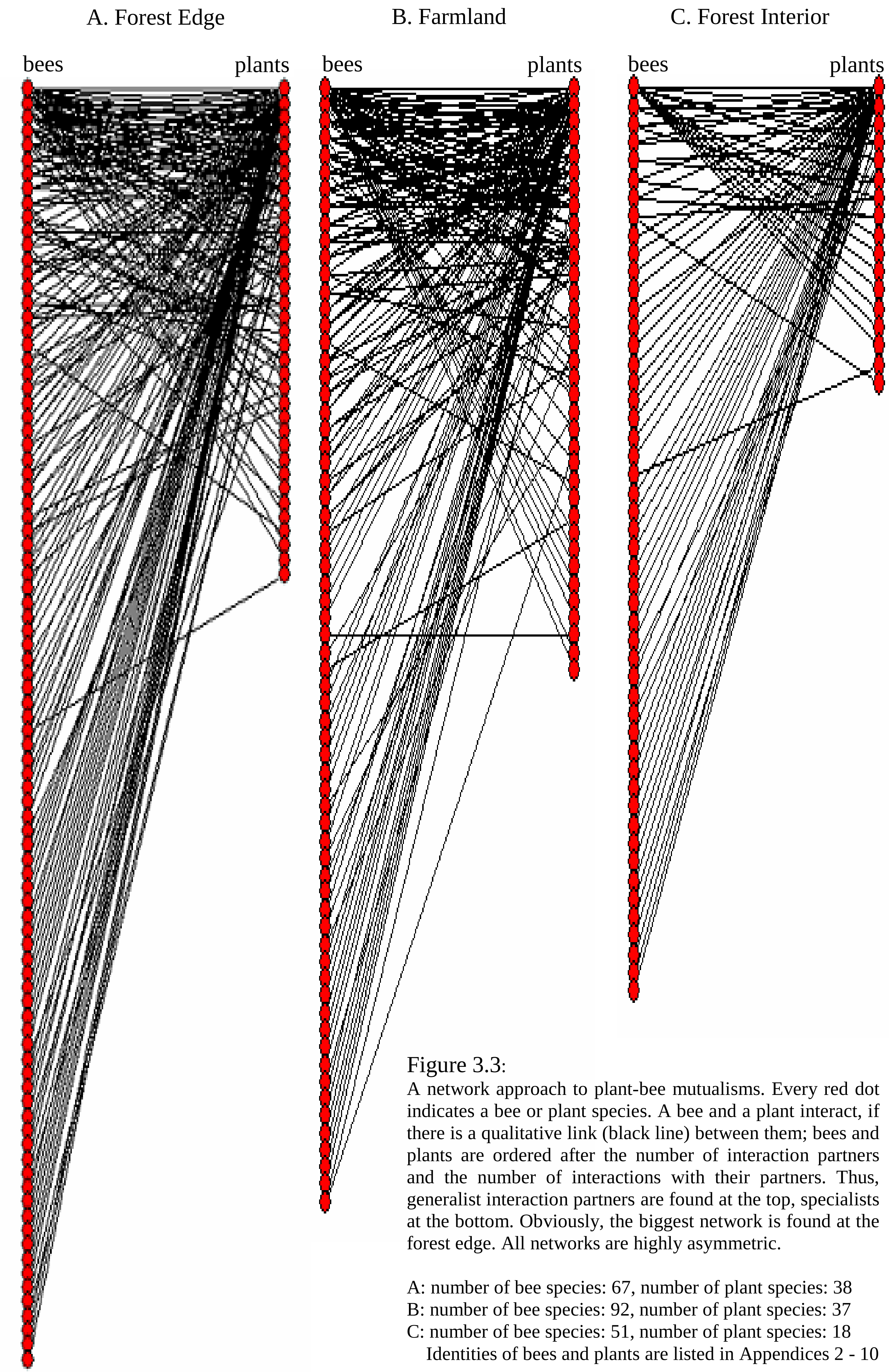
Although the highest number of flower visits was found in the farmland (farmland: N = 1897, forest edge: N = 1387, forest interior: N = 700), highest number of recorded interactions was found at the forest edge (forest edge: I = 194, farmland: I = 160, forest interior: I = 69) as well as the biggest network (forest edge: M = 3404, farmland: M = 2546, forest interior: M = 918; Figure 3, Table 3.5). Highest connectance was found in the forest (forest: C = 20.16, forest edge: C = 9.45, farmland: C = 10.83). The mean number of interactions across bee species (lm_{Bee}) as well as plant species (lm_{Plant}) was highest in the farmland compared to the other two habitat types (farmland: lm_{Bee} = 2.52, lm_{Plant} = 2.28, forest edge: lm_{Bee} = 2.16, lm_{Plant} = 1.95, forest interior: lm_{Bee} = 1.55, lm_{Plant} = 0.80).

The flower visitor web patterns differed highly between seasons. While the biggest network in the farmland was found in the long rain season (M = 682), smallest web and highest connectance values were found in the short rain season (M = 405, C = 12.09). At the forest edge the biggest network was found in the cold dry season (M = 987), while smallest network and highest connectance appeared in the dry season (M = 440, C = 14.54). The biggest network inside the forest was found in the cold dry season (M = 320), the smallest network and highest connectance in the long rain season (M = 27, C = 29.63, Table 3.5, for details see Appendices 3.2-3.10).

Table 3.4:
Morisita-Horn Similarities of the flower visiting bee species in the different habitats and seasons; (A) all bee species, (B) solitary bee species only (lr = long rain season, cd = cold dry season, sr = short rain season, d = dry season

A		farmland				forest edge				forest		
		lr	cd	sr	d	lr	cd	sr	d	lr	cd	sr
farmland	cd	0.969									🟥	>0.95
	sr	0.988	0.968								🟧	>0.90
	d	0.991	0.989	0.983							🟨	>0.85
forest edge	lr	0.978	0.991	0.971	0.988							<0.849
	cd	0.761	0.861	0.772	0.803	0.850						
	sr	0.908	0.955	0.905	0.933	0.959	0.874					
	d	0.995	0.979	0.979	0.993	0.988	0.786	0.939				
forest	lr	0.991	0.937	0.970	0.973	0.949	0.706	0.864	0.980			
	cd	0.854	0.917	0.863	0.887	0.908	0.892	0.899	0.871	0.816		
	sr	0.871	0.915	0.875	0.894	0.915	0.850	0.911	0.892	0.837	0.961	
	d	0.985	0.985	0.985	0.989	0.990	0.824	0.933	0.986	0.961	0.911	0.922

B		farmland				forest edge				Forest		
		lr	cd	sr	d	lr	cd	sr	d	lr	cd	Sr
farmland	cd	0.614									🟥	>0.75
	sr	0.489	0.446								🟧	>0.50
	d	0.609	0.829	0.367							🟨	>0.25
forest edge	lr	0.894	0.589	0.420	0.550							<0.249
	cd	0.501	0.522	0.304	0.367	0.572						
	sr	0.675	0.441	0.252	0.465	0.619	0.276					
	d	0.796	0.541	0.277	0.557	0.747	0.301	0.902				
forest	lr	0.480	0.447	0.257	0.402	0.529	0.533	0.366	0.411			
	cd	0.102	0.170	0.130	0.200	0.109	0.260	0.074	0.055	0.529		
	sr	0.113	0.074	0.028	0.082	0.132	0.132	0.234	0.221	0.369	0.690	
	d	0.538	0.378	0.258	0.354	0.590	0.462	0.250	0.386	0.465	0.545	0.537



A. Forest Edge

B. Farmland

C. Forest Interior

Figure 3.3:
A network approach to plant-bee mutualisms. Every red dot indicates a bee or plant species. A bee and a plant interact, if there is a qualitative link (black line) between them; bees and plants are ordered after the number of interaction partners and the number of interactions with their partners. Thus, generalist interaction partners are found at the top, specialists at the bottom. Obviously, the biggest network is found at the forest edge. All networks are highly asymmetric.

A: number of bee species: 67, number of plant species: 38
B: number of bee species: 92, number of plant species: 37
C: number of bee species: 51, number of plant species: 18
Identities of bees and plants are listed in Appendices 2 - 10

Quantified visitation rate

The quantified visitation rates were calculated for each habitat, taking into account the influence of the abundance of bees as well as plants on the pattern of interactions. The total quantitative flower visitor webs of farmland and forest edge were of more than double the size of the flower visitor web found inside the forest (farmland: Q_{total} = 24270, forest edge: Q_{total} = 22648, forest interior: Q_{total} = 10844; Table 3.5).

After subdividing the data into seasonal units, the flower visitor webs in farmland and at the forest edge were biggest in the short rain season, while the biggest web inside the forest was found in the cold dry season (farmland: $Q_{short\ rain}$ = 9480, forest edge: $Q_{short\ rain}$ = 14001, forest: $Q_{cold\ dry}$ = 8773; Table 3.5). The quantified visitation rate differed highly between seasons, especially inside the forest, where the flower visitor web size of the cold dry season built 80.1% of the whole year's quantified network. Differences in size between the seasons in the other two habitat types were significantly lower, with the short rain season building 39.1% in the farmland and 61.8% at the forest edge.

Table 3.5:
Structure of the flower visitor webs in the different habitats and seasons (M = network size, C = connectance, L_{mPlant} = no. interactions across plant species, $L_{maxPlant}$ = no. interaction partners of the most-connected plant species, L_{mBee} = no. interactions across bee species, L_{maxBee} = no. interaction partners of the most-connected bee species

	season	M	C	L_{mPlant}	$L_{maxPlant}$	L_{mBee}	L_{maxBee}	Quant visit.rate
Farmland	long rain	682	10.41	3.23	11	2.29	17	6901
	cold dry	504	10.71	3.68	16	1.50	9	5607
	short rain	405	12.09	3.26	14	1.81	11	9480
	dry	465	10.11	3.13	20	1.52	10	2282
	all seasons	2546	10.83	2.28	39	2.52	25	24270
forest edge	long rain	880	7.39	3.25	28	1.48	8	1668
	cold dry	987	7.49	3.52	26	1.57	13	3812
	short rain	777	8.37	3.20	16	1.76	12	14001
	dry	440	14.54	6.40	32	1.45	5	3167
	all seasons	3404	9.45	1.95	59	2.16	20	22648
Forest	long rain	27	29.63	3.00	6	1.00	2	223
	cold dry	320	11.88	3.80	25	1.19	8	8773
	short rain	280	10.36	2.07	12	1.45	8	913
	dry	80	28.75	5.75	19	1.15	3	935
	all seasons	918	20.16	0.80	40	1.55	11	10844

M = network size, C = connectance, L_{mPlant} = no. interactions across plant species, $L_{maxPlant}$ = no. interaction partners of the most-connected plant species, L_{mBee} = no. interactions across bee species, L_{maxBee} = no. interaction partners of the most-connected bee species

Measure of nestedness – asymmetry of the flower visitor webs

Nestedness organizes the community in a highly asymmetric way, with specialist species interacting only with generalist (and so less fluctuating) species and generalist species interacting with generalist as well as specialist species.

In all three habitat types, flower visitor webs were highly nested (farmland: N = 0.975, forest edge: N = 0.976, forest: N = 0.967; Figure 3.4) and the interactions among species thus asymmetrically organized. The networks departed highly significantly ($p < 0.001$) from randomly assembled webs (Table 3.6), and thus, a large number of species with few interactions coexisted with a relatively small number of "super"-generalists. Nestedness increased with the complexity (number of interactions) of the network: for a given number of species, communities with more interactions were significantly more nested.

Table 3.6:
matrix temperature and nestedness of the bee-flower communities in the different seasons and habitats

Habitat type	Season	matrix temperature	nestedness	no. of species	averg. matrix temperature
Farmland	long rain	9.85°	0.901***	53	24.73°
	cold dry	10.07°	0.899**	50	21.84°
	short rain	6.56°	0.934**	42	24.53°
	dry	5.44°	0.946**	46	20.49°
forest edge	long rain	10.11°	0.899^{ns}	64	14.50°
	cold dry	6.17°	0.938***	68	19.72°
	short rain	6.01°	0.931**	58	18.78°
	dry	14.91°	0.851**	54	32.57°
Forest	long rain	21.15°	0.789^{ns}	12	21.25°
	cold dry	4.01°	0.960***	42	24.68°
	short rain	9.05°	0.910*	34	17.42°
	dry	3.27°	0.967**	24	37.42°
Farmland	all seasons	2.40°	0.976***	105	18.23°
forest edge	all seasons	2.46°	0.975***	129	16.68°
forest	all seasons	3.25°	0.968***	69	19.14°

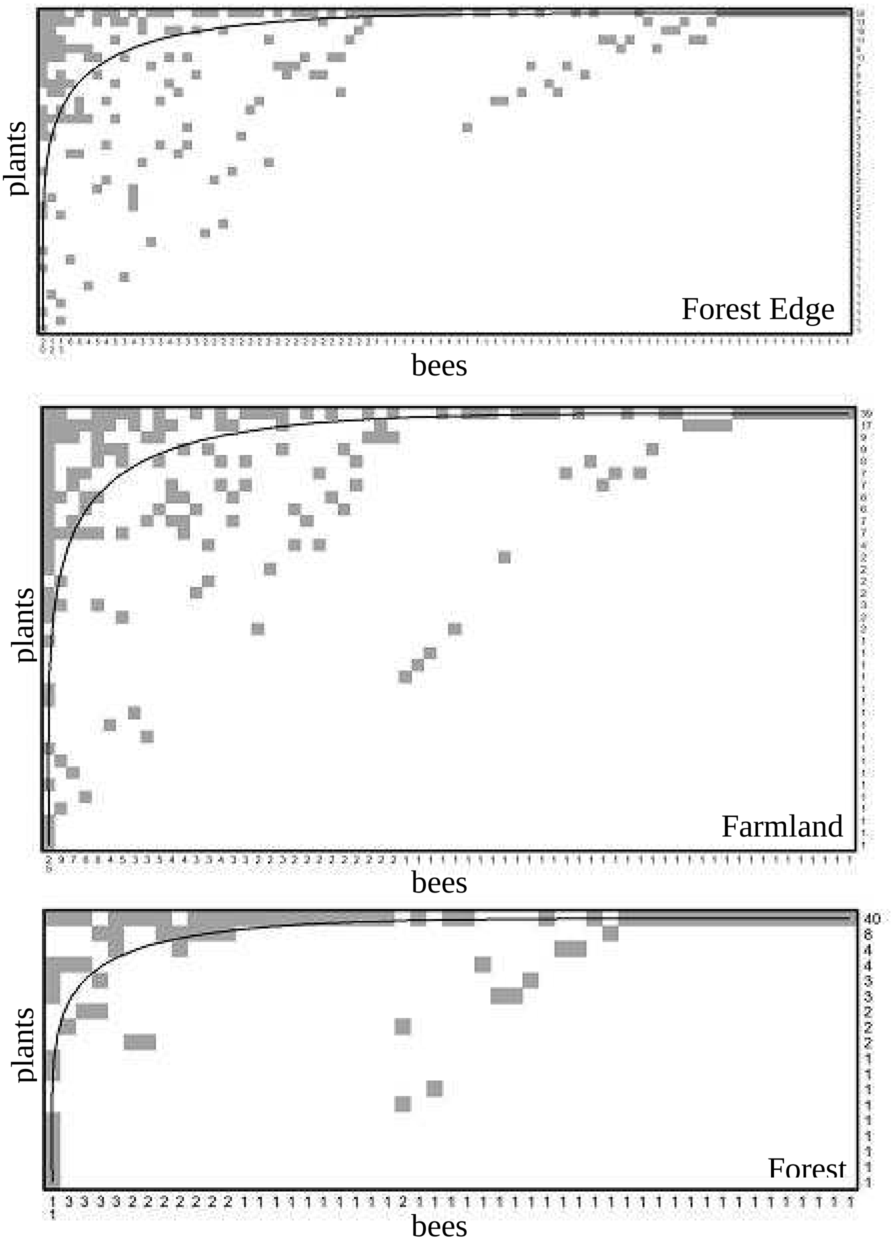


Figure 3.4:
Nestedness calculation of the bee-plant interactions in the three habitats farmland, forest edge, forest interior; the values of nestedness were N = 0.975 (forest edge), N = 0.976 (farmland), N = 0.968 (forest). Numbers label bee and plant species, which are ranked in decreasing number of interactions per species. A filled square indicates an observed interaction between plant species I and animal species j. the line represents the isocline of perfect nestedness. On a perfectly nested scenario, all interactions would lie before the isocline (on the left side).

3.5 Discussion

3.5.1 Community structure

The investigations were conducted in three habitat types, which differed in their plant composition and vegetation structure. Although the numbers of plant species I found in each habitat were rather similar, the proportion of flowering species differed highly, with the forest interior presenting the smallest number of flowering species. However, the number of plant species involved in interactions was rather small in all habitats. While 32% of the flowering species were involved in interactions in the farmland, only 24% respectively 12% were involved at the forest edge and inside the forest. Although the total number of flowering plant species was higher at the forest edge, the number of plant species involved in interactions did not differ from the farmland. As some plant species had only very few numbers of flowers, they might have been not attractive enough for flower visiting bees as other plant species showed bigger floral displays and thus provided the bees with bigger food resources. Furthermore, I observed high numbers of singletons (bees which occurred only once in a habitat during the whole observation period) especially at the forest edge and inside the forest. These possibly rare species tended to visit the most generalized and abundant plant species, ignoring plants with smaller amounts of flowers and a rather patchy distribution. However, as observations were conducted at given times of the day only, flowers were possibly visited in the non-observed periods. Furthermore, as I did not investigate the mutualistic interactions between flowers and non-bee flower visitors like flies, beetles or sunbirds, I investigated a subweb only. Thus, plants with flower syndromes not attractive or suitable for bees were counted but were not visited by bees due to the forbidden links (*sensu* JORDANO ET AL. 2003). Furthermore, the flower visitor community of trees was definitely underestimated, because observations were done from the forest floor, and thus the focus was on the understorey plant community.

In its lifecycle, a bee needs several different resources, like nectar, pollen, specific nesting sites or nesting materials (WESTRICH 1996, GATHMANN & TSCHARNTKE 2002). All investigated habitats were richly structured, such that enough nesting sites for bees should have been available in all these habitats. Other factors were of higher influence on the bees' lifecycle, like the food resources (number of flowers) and abiotic factors like temperature and humidity. In this study, the forest edge was the most diverse habitat type in terms of plant as well as bee species richness. As this habitat is characterised by a rather high habitat heterogeneity (large number of different nesting sites), the conjunction with the other habitats, and in this case a great number of flowers as well, it was not surprising to find the highest bee species richness here. Bee species richness correlated with flower abundance, and was thus resource-limited. Consequently, smallest bee species richness and abundance were found in the flower-poor forest interior.

Most flower visitors in all three habitats were extremely rare, and we found a high number of singletons and doubletons (52% with one or two interactions), which was similar to numbers presented by PETANIDOU & POTTS (2006) on species rich Mediterranean pollinator communities.

Spatiotemporal variation in flower visitors

I found clear variation on the seasonal scale in flower abundance as well as diversity and abundance of bees. The increase in bee abundance that I observed in certain seasons according to the habitats was concomitant with higher flower abundance per plot at that time, while the increase in bee diversity was not concomitant with higher flower diversity at that time. Thus, my results differed from TYLIANAKIS ET AL. (2005), who found high Hymenoptera diversity in the seasons with higher flowering herb numbers at that time.

In the farmland, highest abundance of bees was found in the long rain and cold dry seasons. Although this was not the period of highest flower abundance in the study sites, it is the usual flowering season of crops (especially beans and cowpeas) which offer a high amount of flower and thus food supply, and increased this habitat's attractiveness to the bees. At the forest edge, the pattern was divided between social and solitary bees. Social bees were most abundant in the short rain season, when flower abundance was highest. Instead, solitary bees were most abundant in the dry season, the season with the smallest flower numbers. As the numbers of flowers in the other two habitats were even smaller during that season, bees possibly migrated to the forest edge because of the higher food availability there.

The results suggest, that the reduced flower quantity inside the forest shaped not only bee species number of the community, but favoured selectively larger bees. Large bees are able to invade new habitats faster respectively are able to nest far from their forage source due to their greater dispersal ability (GATHMANN ET AL. 1994). Furthermore, HERRERA (1997) found, that due to size related thermal constraints, small bees foraged only under high-irradiance conditions, while bigger bees selected conditions of low irradiance. Thus, variations in pollinator compositions within and between habitats and seasons seemed to be influenced by thermal and resource limitations. These findings imply that although the most important plant species occurred in all habitat types, restrictions for migration are existent.

In all habitat types high rates of spatial turnover were found. Especially inside the forest, the spatial turnover rate explained a high proportion of the γ-diversity. These results suggest, that especially inside the forest, the bee species compositions differ more between study sites compared to the open habitats. This pattern might be caused by (1) different flower displays in different study sites, (2) the overall small bee community inside the forest, and thus just an artefact, (3) the flower-visiting behaviour of the bees inside the forest. Focusing on a single plant species (*Justicia flava*, chapter 3), I found distinct spatial autocorrelation in flower visitor composition as a possible indirect sign for spatial explicit trap-lining behaviour of the bees. The bees' behaviour seemed to result from the small numbers and scattered distribution of flowers, forcing them to fly relatively long distances and to revisit all flowers on the trapline.

While the overall bee species composition was highly similar between the habitats, differences were obvious focusing on the different seasons. Although the temporal turnover rates in all habitat types were relatively low, they did still explain a greater fraction of the γ-diversity than did the α-diversity. Especially the cold dry and short rain seasons at the forest edge and inside the forest, which showed highest bee diversities, were highly dissimilar to bee species compositions in other seasons and habitats. The former two seasons seemed to be most attractive to the bees, most likely because of big flower displays as well as comparably good nesting conditions, especially in the cold dry season (personal observations). Furthermore, the uniqueness of the bee species composition can increase with increasing bee species richness.

46.7% of the overall γ-diversity represented turnover in species between the different habitat types. Thus, the overlap in species composition and diversity between the habitats was high. As all study sites were situated in close vicinity to each other, bees were theoretically in the position to migrate between the study sites. If bees really migrate between extremely different habitats (open farmland versus dense forest) is still not yet proved and needs to be investigated in more detail, e.g. with the help of radio tracking techniques.

3.5.2 Visitation webs

Structure of visitation webs

The three webs were characterized by a few very abundant species and many rare species with small numbers of interactions. Corresponding with the species richness distribution between habitats, I found the smallest visitation web inside the forest, while the biggest network occurred at the forest edge.

The web connectance in all three habitats was relatively high, compared to 29 plant-pollinator systems compiled by OLESEN & JORDANO (2002). As I sampled a subset of a whole web only, this could explain the discrepancy in connectance between this and other studies. The highest connectance and thus the most generalized network (JORDANO ET AL. 2006) were found inside the forest, meaning that each bee species was connected with a relatively large fraction of the plant species and vice versa. Consequently, in the bigger webs in the farmland and at the forest edge, that had lower connectance values, species had a relatively smaller portion of the interactions of the whole network. However, total numbers of interaction partners were higher compared to the forest network (see 3.5.3).

The big flower displays of crop plants (beans, cowpeas) increased the suitability and attractiveness of the open habitats outside the forest extremely. However, the structure of the visitation webs differed between seasons. Due to drought and/or low temperatures, numbers of flowers varied dramatically, leading to decreasing numbers in flower visitors in periods of food scarcity. Especially inside the forest I found high seasonal fluctuations in flower display and consequently in visitation web size. The results emphasize, that it is extremely necessary to create year-long networks from consecutive rather than cumulative data or networks (BASILIO ET AL. 2006). Consecutive webs reflect the pattern of interactions during a discrete time span, and do thus describe interactions only among partners with coincident phenologies, and reveal oscillations in the number of partners and their degree of generalization, and thus changes in the connectance of the system. As I only investigated the time period of one year, I was not able to take into concern annual differences in species richness and abundance of bees and plants which are most likely (HERRERA 1988).

Quantified visitation rate (QVR)

Taking into account not only the qualitative components of the flower visitor web, like web size and number of interaction partners, but also the abundance of bees and flowers, the flower visitor webs in farmland and at the forest edge were double the size of the web inside the forest. Besides other reasons, this was due to the high abundance of social bees which were highly attracted by the big flower displays of the crop plants. Although the qualitative flower visitor network was biggest at the forest edge, QVR was highest in the farmland as abundance of honeybees was very high.

Outside the forest, the seasonal pattern of the quantified visitation rate did not correspond with that of the qualitative flower visitor web size, as highest QVR occurred in the short rain season. The mass flower of different crops in the long rain and cold dry season, in which the biggest qualitative networks were found, might have been the reason. First of all, a mass flower creates a big food supply to the flower visitors. Furthermore, social and solitary bees react differently, as the social bees need to provide their colony with food, while the solitary bees need much smaller amounts of nectar and pollen to provide their nests. Thus, the social bees, which especially influence the QVR, might have shifted during the crop flower into the farms, while the solitary bees might, due to avoidance of competition, stay at the wild flowers. Inside the forest, QVR rate was highest in the cold dry season as was the qualitative network size. However, I found a strong seasonality in both the qualitative and the quantitative component of the network. Inside the forest, the quantitative pollinator web in the cold dry season built more than 80 % of the year's web, whereas seasonal differences in the other habitats were much smaller. It seemed like abiotic factors, especially comparatively low temperatures and high humidity influenced the flower production as well as the activity pattern of the flower visiting bees inside the forest most. Especially in the rainy seasons, temperatures are usually very low, and flowers, fruits and bee-nests were found moulding (personal observations).

3.5.3 Key species and generalization

In this study, plants tended to be more generalistic compared to the bees. This pattern might be an observation artefact as observations on interactions were done focusing on the plant respectively their flowers rather than focusing on the visiting insects.

Although the most generalized flower visitor network was found inside the forest, the species with the most interactions partners (= the most generalized species) occurred in the farmland. The three most important plant species in each of the three habitat types were involved in more than 50% of the observed interactions. These species interacted with at least 36% of all animal species and were thus the "supergeneralists" of this study (farmland: 39.4%, forest edge: 36.4%, forest interior: 60.1%) Especially the herbal plant *Justicia flava* was found to be a keystone species. Flowers of this plant were found throughout the year in every habitat, which made it an important nectar resource for the bees. *Bidens pilosa* and *Tithonia diversifolia*, the other two dominant species in the farmland, showed the same pattern in their flowering phenology. At the forest edge and inside the forest, two of the three plant species showed also a year through flowering phenology, but in each habitat one species showed seasonal flowering patterns (forest edge: *Cordia abyssinica*, forest: *Harungana madagascariensis*). Therefore, the problem of forbidden links was more acute in these habitats.

The three most important bee species were involved in more than 65% of the observed interactions. Especially the bee species *Apis mellifera* and *Meliponula bocandei* showed a high linkage level. These long-lived eusocial groups interact with a greater fraction of the available flowers (ROUBIK 1980) because a greater turnover of flower species during their longer flight periods promotes "sequential specialization" (HEINRICH 1979) in contrast to solitary bees with short activity periods (CRUDEN 1972). The three most important bee species interacted with at least 17.5% of all plant species (farmland: 19.4%, forest edge: 17.5%, forest interior: 21.7%). The most dominant bee species was the honeybee *Apis mellifera,* which was found in high abundances in all habitat types. This indigenous species was responsible for the highest proportion of interactions in all three webs. While it's proportion of links at the forest edge was 10.3%, the proportion increased with decreasing web size (farmland: 15.6%, forest interior: 21.7%). The results suggest that as the networks become increasingly diverse, each species "dilutes" its interaction strength because it interacts with a smaller fraction of the available partners and because the average dependence decreases as the absolute number of mutualists increases. These findings concurred with earlier findings of pollination networks (JORDANO 1987, OLESEN & JORDANO 2002).

Some of the most important plant and bee species were highly linked in all habitat types, while others, like *Tithonia diversifolia* and *Cordia abyssinica* were restricted to the farmland respectively the forest edge. In all habitats very high numbers of rare species were characteristic (proportion of bees and plants, which occurred only once or twice over the whole observation period; bees (plants): farmland: 31.9% (14.4%), forest edge: 37.9% (37.9%), forest interior: 87.2% (17.4%))

Asymmetry of the flower visitor webs

The networks in this study showed high nestedness. These findings concurred with earlier findings of pollination networks (e.g. BASCOMPTE ET AL. 2003). Nested networks are highly cohesive; that is, the most generalist plant and animal species interact among them generating a dense core of interactions to which the rest of the community is attached. Thus, a species is more unlikely to become isolated of the network after the elimination of other species when embedded on such a highly cohesive network. Second, nestedness organizes the community in a highly asymmetrical way, with specialist species interacting only with generalist (and so less fluctuating) species. This asymmetrical pattern can provide pathways for rare species to persist. Nestedness organizes complex coevolving networks in a specific way between highly specialized pairwise coevolution and highly diffuse coevolution. It results in both a core of taxa that may drive the evolution of the whole community, and in asymmetric interactions among species with different specialization levels. Furthermore, the seasonal and spatial variation, and the resulting existence of forbidden links limits the growth of interaction networks, and confers then broad-scale behaviour. Thus, nested networks show potential implications for community persistence, as they are more robust to the eventual loss of keystone species, which are the backbone of the interactions (JORDANO ET AL. 2003).

In this study, I found bigger flower visitor networks outside the forest in habitats which on one side were more disturbed than the forest but on the other hand offered higher amounts and a better seasonal distribution of resources to the bees compared to the forest. Thus, in this highly structured forest-farmland mosaic, bees seemed to be highly limited by resources rather than directly by other factors of habitat quality. However, to offer a sufficient amount of floral resources to the flower visiting bees, landscapes need to stay structured and diverse, as the amount of food resources will decrease with increasing monotony of the farmland.

The seasonal variation was highest inside the forest, while the different seasons were more similar in the other two habitats. Thus, these open areas might work as a reservoir in periods of very small flower amounts inside the forest and bees could be able to move between farmland and forest, which needs to be investigated in future. Furthermore, as I found a high spatial overlap in bee species composition between the different habitats, conserving not only the forest-nature-reserve but also the structure of the surrounding farmland, and thus the whole landscape mosaic, is an important step in conserving bees and the ecosystem service pollination.

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4. *JUSTICIA FLAVA* (ACANTHACEAE): INFLUENCE OF DIVERSITY AND ABUNDANCE OF FLOWER VISITORS ON THE REPRODUCTIVE SUCCESS

4.1 Abstract

Destruction and fragmentation of landscapes can lead to reduction in species richness and abundance of pollinator guilds and thus to a reduction in the reproductive success of plants relying on pollination by these animals.

I investigated the pattern of diversity and abundance of flower visitors of an abundant herbal plant species, *Justicia flava* (Acanthaceae) in a tropical agriculture-forest mosaic in Western Kenya. Furthermore I analysed the influence of diversity and abundance of the flower visiting insects on the reproductive success of this self-incompatible plant.

The flowers were visited by 74 species of insects in total, but only by 2-19 species per study site. While highest species richness was found in the farmland, highest diversity (species richness + eveness) was found inside the forest. Due to a high dominance of honeybees, the abundance of flower visitors outside the forest was extremely high. Up to a distance of 1500m from the forest, the number of bee species visiting the flowers of *Justicia flava* decreased significantly with increasing distance from the forest whereas the flower visitor composition on study sites farther from the forest did not show any dependency on the distance.

The reproductive success of the self-incompatible plant was neither influenced by the diversity nor by the abundance of flower visitors, due to the fact, that *J. flava* seemed to be a keystone food resource for several bee species and thus experienced high visitation frequencies. Thus, the plant was not pollinator-limited, but rather resource-limited due to a very dry observation season. Even if diversity and abundance of pollinators did not show any direct influence on the fruit and seed set of *Justicia flava* in this rather short observation, the composition and plant communities are of great importance for the long term preservation of maintenance of plant pollinator systems.

4.2 Introduction

The decline of biodiversity and its effect on the composition of ecosystems and the interactions between organisms and populations is one of the most urgently researched and discussed topics in ecology. CHAPIN ET AL. (1997) highlighted human-induced changes in biotic diversity and alterations to the structure and functioning of ecosystems as the two most dramatic ecological trends of the past century. Especially land-use practices, like intensification of agricultural land use, deforestation, urbanization and overexploitation strongly affect species composition and diversity. Thus ecosystems suffer not only directly through changes in ecosystem processes (like productivity, nitrogen mineralization rate, etc.). Moreover a loss of differential environmental sensitivity, which is important for an ecosystem's ability to react to a changing environment (e.g. climatic changes), is the consequence. This loss is caused by a loss of genetic and species diversity. To understand how changes in species composition affect ecosystem processes and services is currently a major aim of ecology (FONTAINE ET AL. 2006), and links between species and ecosystem processes are emerging as a problem of fundamental concern (CHAPIN ET AL. 1997).

Pollination is an ecological process involving 90% of flowering plant species by some estimates (NABHAN & BUCHMANN 1997) and providing for 15%-30% of the worlds nutrition (O'TOOLE 1993, ROUBIK 1995, KREMEN ET AL. 2002, KLEIN ET AL. 2006). The loss of native habitats threatens natural plants as well as their mutualistic visitors, and thus affects the agricultural production by degrading the services of pollinators (FOLEY ET AL. 2005).

The mutualistic interactions between plants and their pollinators are manifold and highly complex. The rates of visitation of pollinators may vary in relation to various features of floral design, e.g. flower colour (KAY 1978, WASER & PRICE 1981, STANTON 1987, USHIMARU 2007), size (BELL 1985, ECKHART 1991, CONNER & RUSH 1996), nectar production (MITCHELL 1994), floral morph (WOLFE & BARRETT 1987, HUSBAND &BARRETT 1992), and gender in unisexual species (KAY ET AL. 1984, AGREN ET AL. 1986, SCHEMSKE ET AL. 1996). Insect visitation may also be significantly influenced by the display size, the spatial and temporal arrangement of flowers in the floral display (HANDEL 1985, KLINKHAMER & DE JONG 1990) and in a given neighbourhood (FEINSINGER ET AL. 1991, KUNIN 1993). Thus, diversity of pollinators plays a fundamental role in the response to changing environmental conditions. Flower displays that only attract single species, may be subject to periods of extremely low visitation, if these visitor species recruit to other foraging locations (a behaviour that can be observed in several eusocial bee species). Pollination services provided by a diverse pollinator community are less sensitive to changes in the behaviour or abundance of individual species and are more likely to remain stable under changing climate conditions, e.g. as pollinator species replace each other along a temperature gradient according to their thermal preferences (WILLMER 1983, JOHNSON & STEINER 2000, GHAZOUL 2006).

Besides these indirect effects of pollinator diversity through compensation of temporal and spatial variation and a possibly higher cross-pollination rate through differences in pollination behaviour, there is also a potential direct effect through an increase in fruit and seed production with increasing diversity of pollinators. Pollination limitation has usually been related to the visitation rate or abundance of pollinators (KUNIN 1993, LARSON ET AL. 1999, HERRERA 2000, MORANDIN ET AL. 2005). Only few recent studies are dealing with the direct influence of pollinator diversity on the reproductive success of plants. KREMEN ET AL. (2002) found, that diversity was essential for sustaining the pollination service for the watermelon (*Citrullus lanatus*) in the American agricultural system, because of the year-to-year variation in bee community composition and abiotic factors (e.g. climatic). The fruit set of coffee (*Coffea arabica*) increased with the diversity of pollinating bees (KLEIN ET AL. 2003), revealing the influencing effects of changes in pollinator composition on the reproductive success of plants. The studies conducted by KREMEN ET AL. (2002) and KLEIN ET AL. (2003) focused on crop plants, which represent a non-native mass flowering food source for flower visitors in the landscape. Whether there is a direct effect of abundance and diversity of flower visitors on the reproductive success of wild plants, I analysed the pollination system of an entomophilous herb, common to several habitats in an agriculture-forest mosaic in western Kenya. I investigated the different habitat types, and the influence of biotic as well as abiotic factors (e.g. flower display, plant diversity, canopy cover, soil fertility etc.) on the pollination system.

4.3 Material and Methods

4.3.1 Study area and study sites

Study area was the Kakamega Forest, a tropical rain forest and it’s surrounding agricultural areas. The forest is located in western Kenya (0°17’N, 34°54’E) at an altitude of 1,500 m to 1,700 m, about 50 km north of Lake Victoria.

Study sites

The study was conducted on 35 study sites, which were ten by ten metres square and located inside and around the northern part of the forest. The sites were situated in the three different habitat types farmland, forest edge and forest interior. The study sites differed in structural parameters and, thus, complexity, ranging from closed rainforest over bushlands and grasslands to a highly structured farmland mosaic. Five sites were situated inside the forest, eight at the forest edge, and 22 in the surrounding farmland in different distances to the forest. For the analysis of differences in flower visitor composition and reproductive success of *Justicia flava* in the different habitat types, average rather than total values were used, as numbers of study sites differed between habitat types.

4.3.2. *Justicia flava* (Forssk) Vahl (Acanthaceae)

Justicia flava is a self-incompatible herbal plant, common to a variety of habitats in East African highlands (Figure 4.1: distribution in Kenya). The floral syndrome is adaptive to bee pollination, but also a variety of butterflies belong to the flower visitors. Nectar is the only reward to the flower visitors, what makes the flowers also very attractive to male and parasitic bees. Flowers of *Justicia flava* can be found throughout the year, which makes it an important food resource to many insects. The fruits contain maximally four seeds and open with an explosive mechanism, dispersing the seeds in the close vicinity.

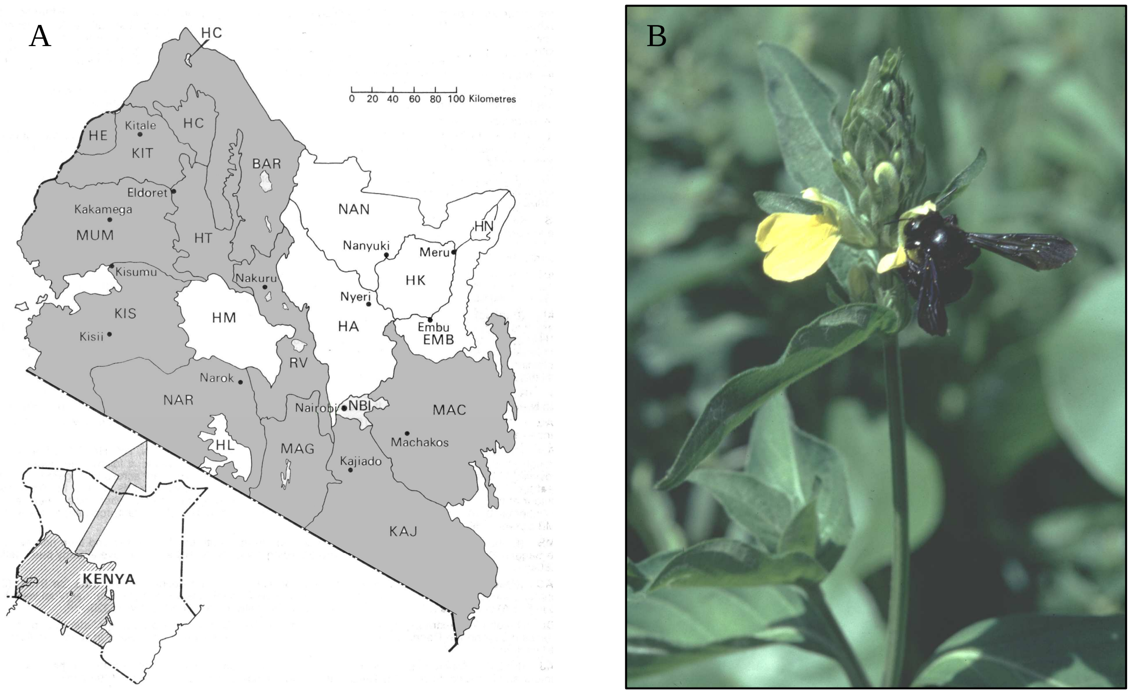

Figure 4.1:
(A): Distribution of *Justicia flava* in the highlands of Kenya, grey colours: distribution, occurrence proved (from: Agnew & Agnew 1994);
(B) *Justicia flava* with *Xylocopa* sp. (photo by Manfred Kraemer)

4.3.3 Considered biotic and abiotic factors

The following biotic and abiotic factors were considered during the analysis of the pollinator systems.

Plant species composition

The plant species composition was investigated prior to flower visitor observations, and all plant species occurring in the study sites identified at least to genus and most of them up to species-level (identification keys: AGNEW & AGNEW 1994, BEENTJE 1994).

Canopy cover

The cover of canopy, giving shade to the herbal layer and thus the focal plant, was estimated using a percentage scale (from 0% = no canopy to 100% = complete canopy coverage). This canopy cover in each study site was used for analysing potential influence of the shade effect of the canopy cover on the visitation frequency.

Number of flowers per study site

Parallel to the flower observation units all flowers of *Justicia flava* as well as of all other plant species on the study sites were counted, to measure the potential influence of food supply on the behaviour of the flower visiting insects (visitation frequency, duration of stay on the site).

Distance to the forest edge

The GPS-coordinates of all study sites were taken, and the distance to the nearest forest edge was calculated with ArcGis 8.0 on the basis of Landsat 7 (ETM+) satellite images (band combination 5/4/3, contrast enhanced). These data were provided by Gertrud Schaab (BIOTA E02, University of Applied Science, Karlsruhe).

Cloudiness

The cloud cover was estimated using eighths (from 0 = no clouds to 8 = full cloud cover). The average cloudiness of all units in each study sites was used for analysing potential relations between visitation frequency and cloudiness.

Windspeed

The windspeed was also estimated using eighths (from 0 = no wind to 8 = strong wind). The average windspeed of all units in each study site was used for analysing potential relations between visitation frequency and windspeed.

Soil parameters

Soil samples of the upper soil horizon were taken from all study sites in January 2005. PH-value, electrical conductivity (EC) and the amount of cations (K^+, Ca^{2+}, Mg^{2+}) from water extracts were measured in the laboratory. Water extracts the water soluble ions and indicates the amount of nutrients available to a plant at all time.

4.3.4 Flower visitors of Justicia flava

The monitoring on the composition of flower visitors of *Justicia flava* was done between January and February 2005. Five observation units were conducted on each of the 35 study sites. Flower visitation observations were done in 30 min units between 10.00 am and 02.00 pm on sunny days. In every observation unit, ten flowers were observed; every visitor, the number of flowers it visited, and the flower visit duration were recorded. These data provided the basis for the calculations of species composition, the abundance and diversity of the flower visitors. After each observation unit, the numbers of conspecific and non-conspecific flowers in the study sites were counted, and flower visitors were caught for 10 minutes with a sweep net for later identification. It was not possible, to identify some of the very small visitors up to species level in the field. In order to avoid interfering with the flower visiting behaviour of the bees, I grouped small bees in 12 groups (Appendix 4.1).

Identifications of the flower visiting bees were done by two specialist taxonomists for African bees. Dr. Mary Gikungu (National Museums of Kenya, Nairobi, Kenya) worked on the families Megachilidae and Halictidae, and Dr. Connal Eardley (Plant Protection Research Institute, Pretoria, South Africa) identified the specimens belonging to the Apidae.

Flower visitor diversity

The between-habitat-diversity of flower visitors was calculated using the Rényi diversity profiles. The use of non-parametric index families allows the diversity of a community to be characterized by a (scale-dependent) diversity profile instead of a numerical value (TÓTHMÉRÉSZ 1998). The first of these techniques, the ‘generalized entropy’, was published by RÉNYI (1961).

$$H_\alpha = \frac{\ln\left(\sum_{i=1}^{s} p_i^\alpha\right)}{1-\alpha}$$

H_α = Rényi Diversity Index
p_i = proportions of each species
α = scale parameter

A profile is calculated by changing the value of α from 0 to infinity. In this thesis, the values of α are: 0, 0.25, 0.5, 1, 2, 4, 8, 16, Inf.

The scale parameter α:

α = 0 => information on species richness; the profile value is the logarithm of the species richness
α = infinity => provides information on the proportion of the most abundant species. Profiles that are higher at α = infinity have a lower proportion of the dominant species.
α = 1 => Shannon diversity index
α = 2 => logarithm of the reciprocal Simpson diversity index

The shape of the Rényi-curve profile is an indication of the eveness. A horizontal profile indicates that all species have the same abundance. The less horizontal a profile is, the less evenly species are distributed. If the profile for one site is everywhere above the profile for another site, then this means that the site with the highest profile is the more diverse of the two. If the profiles intersect, it is not possible to order the sites from lowest to highest diversity (Kindt & Coe 2005). The Rényi diversity profiles were produced, using R 2.4 (The R Development Core Team 2006) and the R package vegan 1.8-3 (Oksanen et al. 2006).

Due to the fact, that there was not a single "diversity-value" for the flower visitor communities of each site, the Rényi diversity index could not be used for further statistical analyses, e.g. the influence on the reproductive success of the plant. Thus, the species richness was used, which was defined here as the number of species, independent of the species' abundance and the community's eveness.

Flower visiting frequency

The rates at which pollinators visit flowers and their patterns of movement between them can affect the success of pollination, gene flow, and the energy budgets of pollinators (Kearns & Inouye 1993). Visitation rates were used as an index of the relative abundance of pollinators, either within or among study sites. In this study, visitation frequency was defined as the number of flower visits per 30-minute time unit.

4.3.5 Reproductive success

I compared the reproductive success of *Justicia flava* in the different study sites and habitat types. In this study, reproductive success was determined as the number of developed fruits and seeds. Germination success and seedling recruitment were not investigated.

Subsequently to the flower visitor observation units, ten flowers per site were marked. After one week, the number of developed fruits (out of the ten marked flowers) was counted and these developed fruits collected. The seeds per fruit were counted in the laboratory; the mean seed set was calculated including the seeds of all developed fruits of each study site.

In this thesis, fruit set is defined as the portion of flowers that developed into fruit; seed set is defined as the portion of seeds that developed per fruit (in *Justicia flava*: maximally 4 seeds per fruit). The reproductive success is the product of fruit and seed set.

4.3.6 Pollination efficiency

The pollination-efficiency observations were done between June and August 2002. Buds of *Justicia flava* were bagged, to prevent unobserved flower visitors. After the flowers reached the female phase they were exposed to a single flower visit, and afterwards covered with mosquito net again. After seven days, fruit set was investigated, developed fruits collected, and seeds counted. The measurements were done on 261 flowers in total.

Such a direct measure of pollinator effectiveness relying on successful seed production after visitation requires fewer assumptions than an indirect measure, and is intuitively much clearer than more elaborate indirect methods, like counts of pollen grains on an insect's body or the plant's stigma. I calculated the Spears efficiency which is the proportion of unrestrained seed set caused by a single visit of species i corrected by the amount of seed set when visitation occurs and allows comparisons of populations of any animal-pollinated plant species (SPEARS 1983).

Spears efficiency was calculated with the following formula:

$$P_E = \frac{(P_i - Z)}{(U - Z)}$$

P_e = Spears Efficiency

Z = mean number of seeds set / flower by a plant population in the absence of pollinator visits

U = mean number of seeds set / flower by a plant population with unrestrained visitation

Pi = mean number of seeds set / flower by a plant population receiving a single visit from species i

Furthermore, I investigated the mating system of *Justicia flava*. To answer the questions, if the plants are able to self-pollinate, I bagged 10 flowers prior to anthesis each, to investigate the ability of active selfing as well as the potential of geitonogamous pollination. For the geitonogamous pollination experiment I transferred pollen of flowers of the same plant to the stigmas of the bagged flowers. Another 10 flowers were marked and used as open control without any treatment.

4.3.7 Data analysis and statistics

In this study the received data were listed with Microsoft Office Excel 2003 and analysed with SPSS 12.0 for Windows. Normality of data was tested using Kolgomorov-Smirnov Test (DORMANN & KÜHN 2004), and if necessary, data were transformed. Number of bee species and individuals visiting *Justicia flava*, the number of individuals of *Apis mellifera* visiting *J. flava*, and number of flowers of *Justicia flava* were square root transformed prior to analyses.

The nonparametric Mann-Whitney-U Test was used to compare the pollination efficiency values of small and big bees, as data were not normally distributed.

Simple linear regression analysis was conducted, to investigate the direct influence of species richness and abundance of the flower visitors on the reproductive success of *Justicia flava*. To analyze the influence of biotic and abiotic factors on the species richness and abundance of flower visitors as well as on the fruit and seed sets of *J. flava*, I used multiple backwards regression analyses. Predictor variables were sequentially omitted according to their relative reduction of R^2s. Inter-correlation among explanatory variables was investigated with Pearson's product moment correlation (MORGAN ET AL. 2004). In case of correlation coefficient of $|r| < 0.7$, I accepted variables to be uncorrelated enough to be retained together as predictors in models. I used one-way analysis of variance (ANOVA) to determine, if flower visitor composition and reproductive success of *Justicia flava* differed among habitats. When the ANOVA was significant, I used Tukey's HSD test to detect pair wise differences between habitats. The assumption of homogeneity of variance for all ANOVAs presented in this paper was tested using Levene's test (UNDERWOOD 1997).

A result is called significant, if the significance level is $p \leq 0.05$, highly significant, if the level is $p \leq 0.001$ and marginally significant, if $0.10 \geq p \geq 0.05$.

4.4 Results

4.4.1 The flower visitor community of Justicia flava

In total *J. flava* was observed for 87 hours, subdivided into 174 observation units of 30 minutes each. During the observations I recorded 4750 flower visits of insects belonging to 74 species of five insect groups (64 species of bees, 9 butterfly species, one beetle species, three fly species, one ant species, the bee species are listed in Appendix 1), with *Apis mellifera* being most abundant (3523 flower visits, 74.0% of all visits) and thus dominating the visitor community. If *Apis mellifera* was found on the study sites, the share of honeybee visits varied between 3.7% in Salazar B (forest interior) and 99.7% in the farmland site Buyangu D.

Table 4.1:

Overview of the composition of flower visitors (sum of species, mean and standard deviation of flower visits) for all visitor species and for bees explicit. Fruit and seed rates of *Justicia flava*.

	flower visiting insects			flower visiting bees					*Justicia flava*		
study site	number of species	mean number of flower visits/30 min	standard deviation of number of flower visits	number bee species per study site (sum)	mean number of flower visits/30 min	standard deviation of number of flower visits	mean number of flower visits/30 min by *A. mellifera*	standard deviation of number of flower visits *A. mellifera*	fruit rate	seed rate	reproductive success (fruit rate X seed rate)
Bukhaywa A	6	2.99	2.02	5	2.87	0.98	2.77	1.02	0.73	0.18	0.13
Bukhaywa B	4	1.04	0.90	3	0.99	0.82	0.95	1.00	0.84	0.21	0.18
Buyangu A	9	4.60	0.74	7	4.60	0.74	4.13	0.55	0.62	0.16	0.10
Buyangu B	5	4.17	2.14	5	4.17	2.14	2.77	2.75	0.22	0.05	0.01
Buyangu C	7	5.36	1.34	5	5.28	1.18	3.72	0.34	0.73	0.18	0.13
Buyangu D	4	7.27	2.52	2	7.17	2.64	7.12	2.62	0.67	0.17	0.11
Buyangu E	13	5.97	4.76	10	5.87	4.82	5.12	5.75	0.68	0.17	0.11
Buyangu F	12	2.18	1.09	11	2.16	1.06	1.62	0.97	0.59	0.15	0.09
Buyangu Hill A	11	1.45	1.32	11	1.45	1.32	0.00	0.00	0.60	0.15	0.09
Campsite A	9	1.30	0.40	6	1.07	0.22	0.20	0.40	0.52	0.13	0.07
Chevoso A	4	3.87	3.41	4	3.87	3.41	3.47	3.51	0.61	0.15	0.09
Ivakale C	4	1.91	0.58	3	1.88	0.59	1.92	0.61	0.83	0.90	0.75
Kabrasi A	6	3.03	2.19	6	2.98	2.15	2.87	2.21	0.73	xx	xx
Kabrasi B	5	1.32	1.00	5	1.32	1.00	1.15	1.06	0.76	0.19	0.14
Kabrasi D	8	3.50	1.05	6	3.45	0.99	1.97	1.09	0.61	0.15	0.09
Kabrasi E	6	3.85	2.89	6	3.85	2.89	3.72	2.92	0.60	0.15	0.09
Kisere C	5	2.86	1.70	4	2.81	1.72	1.87	0.85	0.73	0.18	0.13
Kisere D	8	1.90	1.51	8	1.88	1.47	1.10	0.74	0.80	0.20	0.16
Kivaywa	9	2.75	1.74	8	2.70	1.71	2.20	1.61	0.48	0.11	0.05
Lukhokho people	6	2.28	1.15	5	2.25	1.15	1.80	1.34	0.46	0.16	0.07
Lukhokho river	18	3.95	2.10	17	3.67	1.68	1.00	1.80	0.64	0.15	0.10
Lukume	4	1.27	1.82	4	1.27	1.82	0.87	1.61	0.60	0.16	0.10
Lusero B	9	2.61	2.23	9	2.61	2.23	2.20	1.91	0.66	0.18	0.12
Lusero C	3	4.15	1.96	2	4.12	1.97	4.10	1.92	0.70	0.15	0.11
Mapera	15	2.38	1.21	9	2.16	1.29	0.72	1.01	0.60	0.13	0.08
Mukangu	3	2.99	0.81	3	2.99	0.81	2.62	0.95	0.54	0.13	0.07
Okumo	6	2.23	1.26	4	2.13	1.19	2.12	1.26	0.54	0.17	0.09
Place M	9	1.99	1.29	6	1.81	1.34	1.37	0.94	0.71	0.03	0.02
Salazar A	19	2.23	1.49	15	1.93	1.52	0.00	0.00	0.67	0.13	0.08
Salazar B	12	0.68	0.29	10	0.60	0.27	0.02	0.05	0.13	0.12	0.02
Shikusa A	11	3.82	1.15	10	3.80	1.18	2.67	1.91	0.50	0.16	0.08
Shikusa B	12	2.80	1.28	9	2.47	1.52	2.02	1.61	0.49	0.16	0.08
Shikutse	8	1.07	0.86	8	1.07	0.86	0.47	0.47	0.66	0.15	0.10
Upper Campsite	3	1.91	1.52	2	1.88	1.54	1.85	1.52	0.65	0.17	0.11
farmland	43	3.15	2.06	35	3.09	2.05	2.48	2.07	0.61	0.70	0.43
forest edge	29	2.92	2.59	25	2.88	2.58	2.46	2.65	0.69	0.73	0.51
forest	40	1.61	1.14	29	1.44	1.12	0.19	0.52	0.50	0.70	0.35

Visitor communities with high proportions of honeybees showed highest abundance of flower visitors, with flower visiting frequencies ranging from 0.6 visits/30 min in Salazar B to 7 visits/30 min in Buyangu D. In only two study sites no honey bees were observed (Table 4.1). Both sites were located inside the forest. Study sites differed highly in visitor species richness with the numbers of species varying between 2 (Lusero C, Upper Campsite, Buyangu D) and 19 (Salazar A) (Table 4.1).

The final model of a backwards regression indicated with a high significance ($R^2 = 0.154$, F(3, 126) = 7.633, $p < 0.001$) that the number of open flowers of *Justicia flava* showed the highest positive influence on the flower visiting frequency, while canopy cover and number of flowers of all plant species showed a negative effect (Table 4.2). The number of flower visitor species was also best explained by the number of *Justicia flava* flowers. Canopy cover and number of co-flowering species resulted in a negative effect on the species richness ($R^2 = 0.165$, F(4, 125) = 6.188, $p < 0.001$, Table 4.3). The goodness of fit for the frequency as well as for the species richness is rather low, due to the great number of factors influencing complex systems under natural conditions.

Table 4.2:
Factors influencing the abundance of flower visitors of *Justicia flava*. Final model coefficients of a backward multiple regression ($R^2 = 0.154$, $F_{(3,126)} = 7.633$, $p < 0.001$; started with n = 7 factors). Dependent variable: number of flower visits (sqrt-transformed)

Variable	B	SEB	β	p
No. *J .flava* flowers (sqrt.)	3.97	1.22	0.29	0.001
Canopy cover	-0.71	0.26	-0.27	0.007
No. flowers total	-0.00015	8.1003E-05	-0.19	0.063

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

Table 4.3:
Factors influencing the bee species richness on *Justicia flava*. Final model coefficients of a backward multiple regression ($R^2 = 0.165$, $F_{(4, 125)} = 6.188$, $p < 0.001$; started with n = 7 factors). Dependent variable: number of visitor species (sqrt-transformed)

Variable	B	SEB	β	p
No. *J. flava* flowers (sqrt.)	2.61	0.76	0.31	0.001
Canopy cover	-0.32	0.16	-0.20	0.049
Wind speed	0.29	0.15	0.16	0.055
No. flowers total	-0.00008	0	-0.18	0.082

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

Distance to forest

Depending on the scale, the number of bees visiting the flowers of *Justicia flava* decreased significantly with increasing distance from the forest. This pattern was true up to a distance of about 1500 m (linear Regression: $R^2 = 0.226$, $p = 0.007$, $F_{(1,29)} = 8.473$), whereas this pattern was not observed on study sites farther from the forest (up to 16 km, linear Regression: $R^2 = 0.016$, $p = 0.45$, $F_{(1,34)} = 0.583$, Figure 4.2).

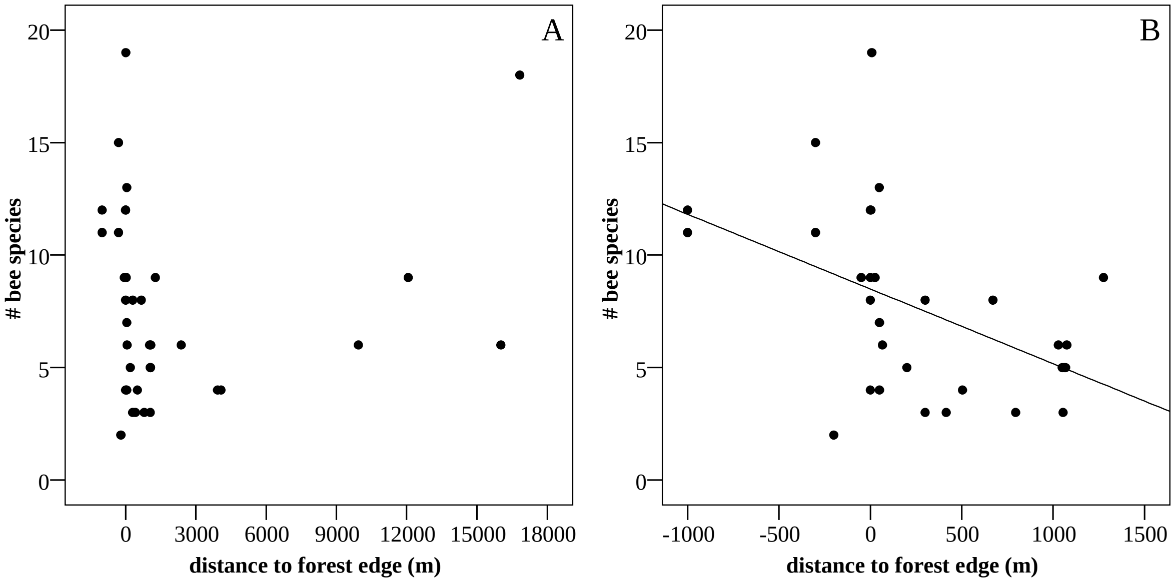

Figure 4.2:
Number of bee species visiting *Justicia flava* in relation to the distance to forest; (A) Distances from -1000m (inside the forest) up to 16000m;
(B) Distances from -1000m (inside the forest) up to 1500m.

Comparing the different habitat types

The composition of flower visitors differed between the three considered habitat types farmland, forest edge and forest interior. Especially at some of the forest edge sites, the frequency of flower visitors reached very high values (up to 7.2 visits/30min of all flower visitors and up to 7.1 visits of bees only, Table 4.1: Buyangu D), and showed low values inside the forest (Salazar B: 0.68 visits (0.6 by bees), Buyangu Hill: 1.45 visits (1.07 by bees)). A statistically significant difference was found among the three habitat types farmland, forest edge and forest interior concerning the species richness of the insect visitors of *Justicia flava* (One-way ANOVA: $F_{(2, 133)} = 5.495$, $p = 0.005$, Figure 4.3, Table 4.4), and also on their abundance (One-way ANOVA $F_{(2, 133)} = 4.76$, $p = 0.01$). Post hoc Tukey HSD Tests indicated, that the number of flower visits as well as the species richness of insects in general and bees in detail were significantly higher in the farmland compared to the forest.

Nevertheless, highest species diversity (species richness plus eveness) was found inside the forest as Rényi diversity profiles indicate (Figure 4.4). If profiles of the Rényi diversity index intersect, comparisons are not allowed. In border-cases, if the intersection occurs very close to zero, as it is the case between the profiles of forest and farmland, this can be discussed (personal communication R. KINDT). Species richness and eveness were lowest at the forest edge.

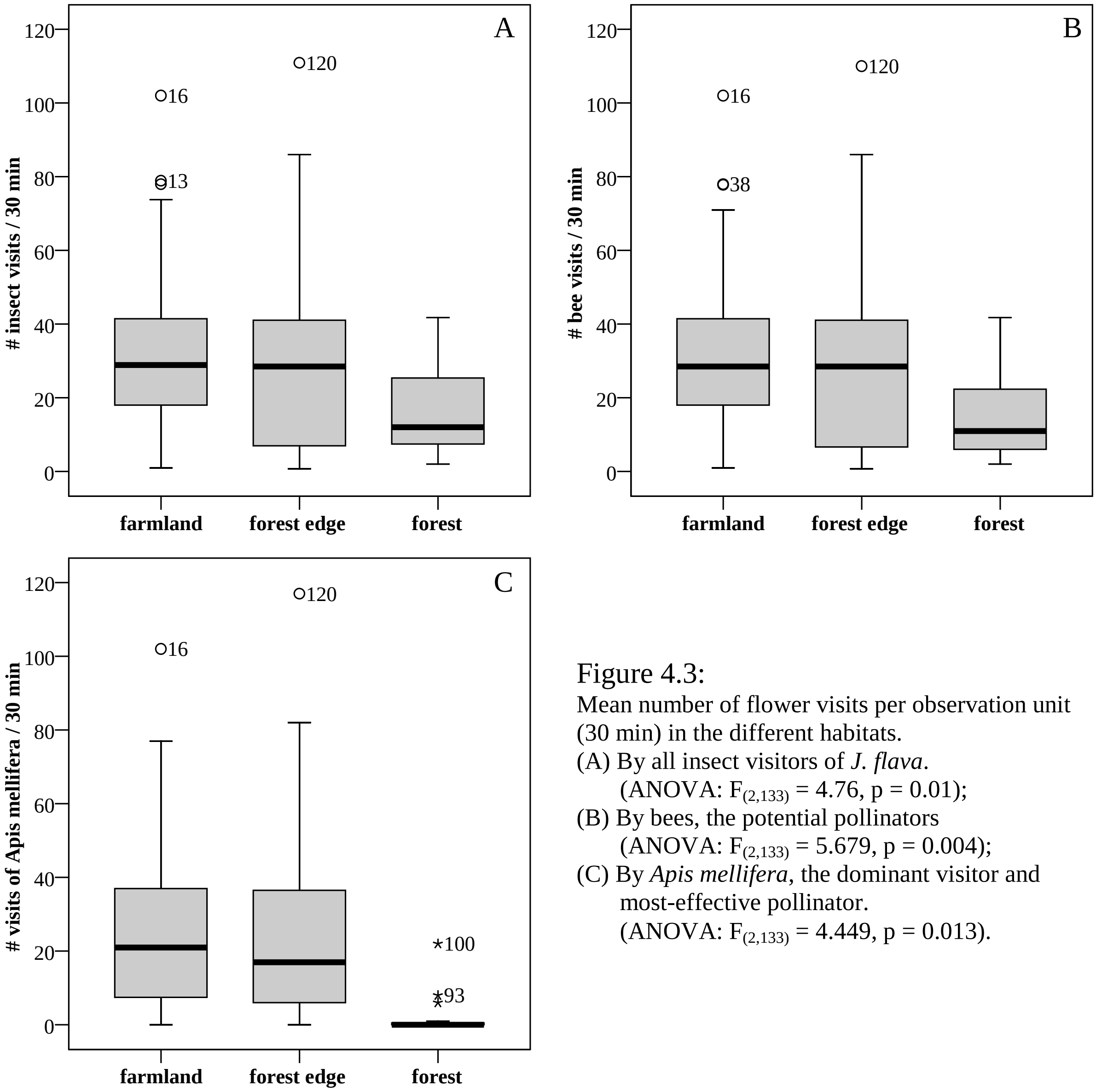

Figure 4.3:
Mean number of flower visits per observation unit (30 min) in the different habitats.
(A) By all insect visitors of *J. flava*.
(ANOVA: $F_{(2,133)} = 4.76$, $p = 0.01$);
(B) By bees, the potential pollinators
(ANOVA: $F_{(2,133)} = 5.679$, $p = 0.004$);
(C) By *Apis mellifera*, the dominant visitor and most-effective pollinator.
(ANOVA: $F_{(2,133)} = 4.449$, $p = 0.013$).

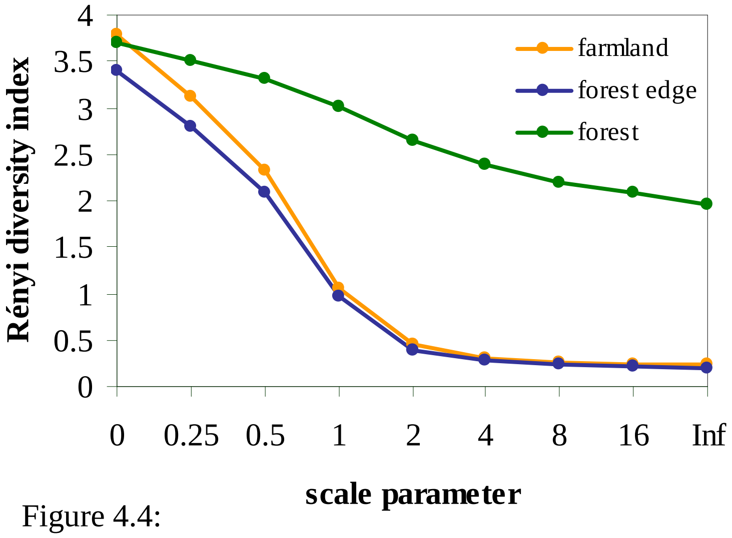

Figure 4.4:
Rényi's diversity profiles. Highest species number was found in the farmland, while highest eveness of flower visitors was found inside the forest (as indicated by the horizontal shape of the profile).

Table 4.4:
One-way analysis of variance summary table comparing the habitat types on species richness and abundance of flower visiting insects, bee species and *Apis mellifera*

source	df	Sum of square	Mean of square	F	p
insect visitors					
no. visits					
between groups	2	37.45	18.73	4.76	0.01
within groups	133	523.07	3.93		
total	135	560.52			
no. visitor species					
between groups	2	16.44	8.22	5.49	0.005
within groups	133	198.96	1.49		
total	135	215.41			
bee visitors					
no. visits					
between groups	2	45.28	22.64	5.68	0.004
within groups	133	530.20	3.99		
total	135	575.48			
no. visitor species					
between groups	2	326.15	163.08	16.07	< 0.001
within groups	133	1350.08	10.15		
total	135	1676.24			
Apis mellifera					
no. visits					
between groups	2	1.99	1	4.45	0.01
within groups	133	29.76	0.22		
total	135	31.75			

4.4.2 Reproductive success

Fruits of *Justicia flava* on the different study sites were collected between 13th of January and 5th of February 2005. In total 1219 flowers were marked and the fruit set of the developed fruits per study site determined. In total 70.0% of the marked flowers produced fruits, and the fruit set ranged between 23% in Salazar B and 88.0% in Bukhaywa B. The overall number of seeds developed was 2.89 out of 4 possible seeds per developed fruit (72.0% seed set). The highest value was found for Ivakale C with 3.60 seeds per fruit (90.0% seed set), and the lowest value in Salazar B with 1.67 seeds per fruit (42.0% seed set). The reproductive success (rs), defined as the mathematical product of fruit and seed set varied strongly and was highest in Ivakale C ($r_s = 0.75$), and lowest in Salazar B ($r_s = 0.02$) (Table 4.1).

Fruit and seed sets in the different habitats

While the differences in seed set and reproductive success (the product of fruit and seed set) did not show any interdependence with the habitat type, the fruit set differed significantly between the habitats (Figure 4.5). Post hoc Tukey HSD Tests indicated that the fruit set at the forest edge was significantly higher (67.0%, $p < 0.05$) than at the other two habitat types (farmland: 61.0%, forest interior: 51.0%). The latter two did not differ significantly from each other.

4.4.3 Pollination efficiency

Studies on the pollination efficiency of the flower visitors of *Justicia flava* showed, that among all flower visiting insects only bees contributed to the plant’s reproductive success. Other flower visitors, mainly butterflies, fed on the flowers’ nectar without touching the reproductive parts of the flowers and were classified as nectar robbers. Thus, I excluded all non-bee visitors from further analysis, and investigated the influence of diversity and abundance of flower visiting bees on the reproductive success of *Justicia flava* only.

Concerning the qualitative (per-single-visit efficiency) as well as the quantitative (abundance) component of the “most-effective-pollinator” principle (definition after SPEARS 1983, HERRERA 1987, 1989), the common and in this area native honeybee *Apis mellifera* was the most effective pollinator of *Justicia flava* (2.87 seeds/fruit after a single flower visit, 74.0% of all flower visits).

Beside this prominent pollinator a trend in the per-visit efficiency was evident, that bigger bees were better pollinators than smaller bees. While a single flower visit of a big bee (body size ≥ 12mm) resulted into a mean seed set of 1.79 seeds per fruit, only an average of

1.27 seeds per fruit were produced after a small bee's (<12mm) flower visit (Mann-Whitney-U Test: U = 3436.5; p = 0.045) (Figure 4.6A) (HAGEN 2003).

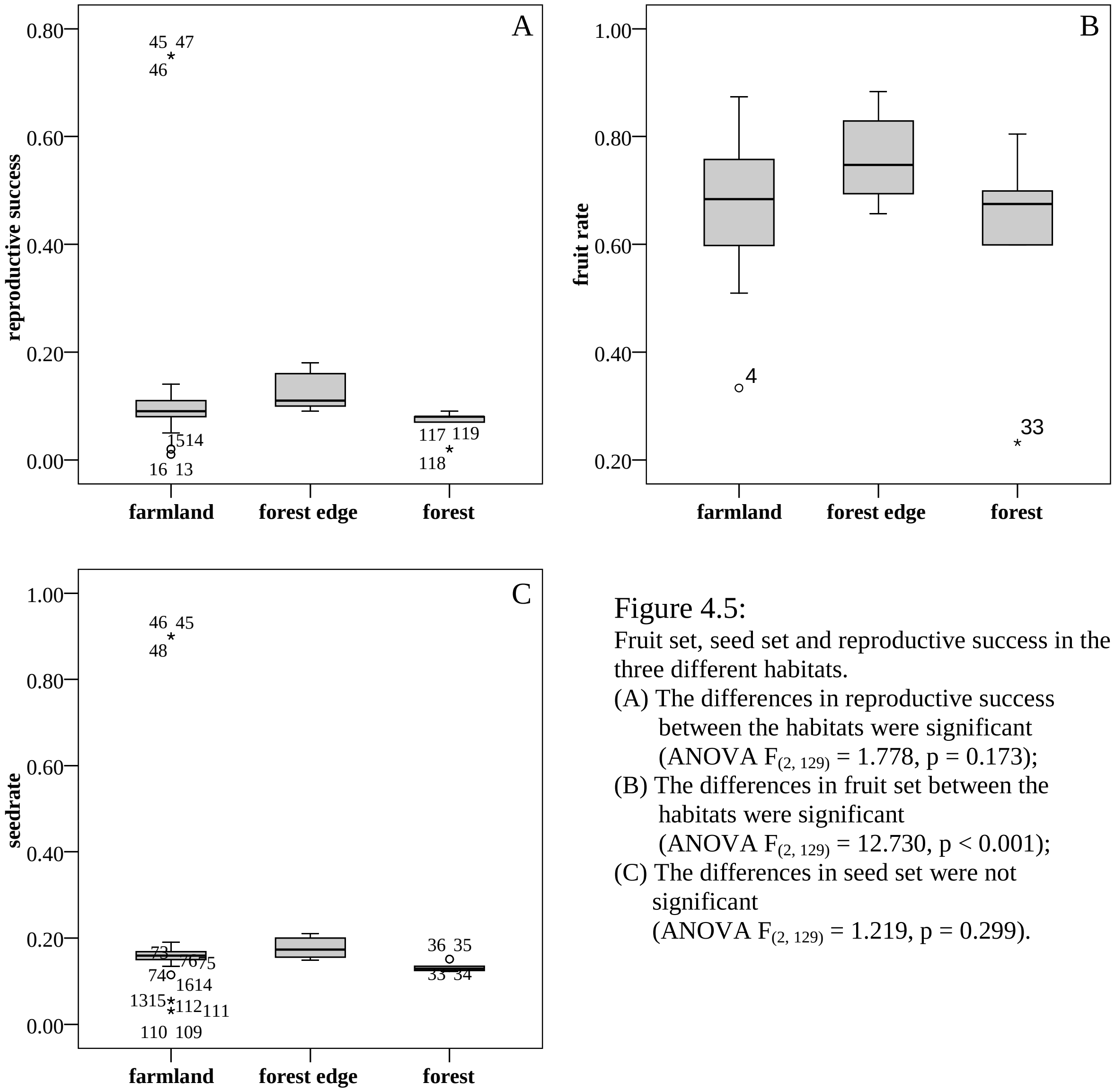

Figure 4.5:
Fruit set, seed set and reproductive success in the three different habitats.
(A) The differences in reproductive success between the habitats were significant (ANOVA $F_{(2, 129)} = 1.778$, p = 0.173);
(B) The differences in fruit set between the habitats were significant (ANOVA $F_{(2, 129)} = 12.730$, $p < 0.001$);
(C) The differences in seed set were not significant (ANOVA $F_{(2, 129)} = 1.219$, p = 0.299).

Self pollination

Without any pollinating vector, the flowers of *Justicia flava* did not produce any fruits and seeds due to the strictly timed separation between anthesis and receptiveness of the stigma. None of the stigmas of bagged flowers received any pollen grains (N = 10), and no fruits were developed, indicating that flowers did not actively self-pollinate. Pollination experiments showed that geitonogamous (neighbour-) pollination was possible but resulted in a lower reproductive success than open pollination. The fruit set of neighbour-pollinated plants was about 51%, and an average of 1.48 seeds per fruit were developed (Figure 4.6B).

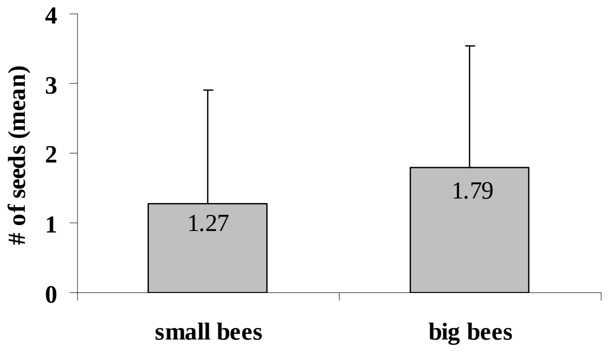

Figure 4.6A:
Pollination efficiency (mean number of seeds after a single flower visit + standard deviation) of small (body length < 12 mm) versus big bees (body length ≥ 12 mm)

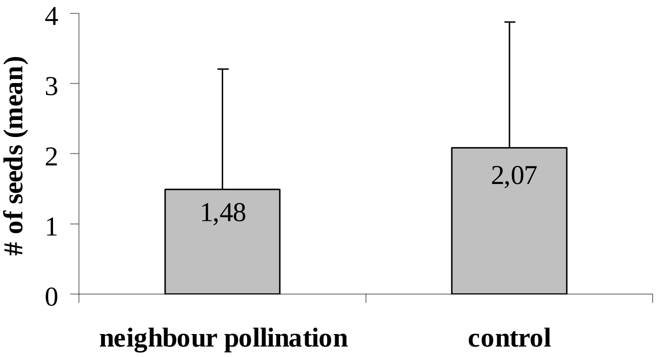

Figure 4.6B:
Number of seeds (mean + standard deviation) after hand-pollination with geitonogamous pollen versus open-pollinated control flowers

4.4.4 Influence of diversity of flower visitors on the fruit and seed set

Due to the fact, that only bees pollinate the flowers of *Justicia flava*, the analysis of the influence of diversity and flower visiting frequency on the reproductive success of *J. flava* was done focusing only on bee-species. Simple linear regressions were conducted to investigate if the species richness and abundance of flower visitors influenced the fruit and seed set of *Justicia flava*. The results were not statistically significant. Bee species richness did not show any influence on the plants' fruit set (Simple Regression: $R^2 = 0.057$, $F_{(1, 134)} = .037$, $p = 0.163$, Figure 4.7A), seed set (Simple Regression: $R^2 = 0.001$, $F_{(1, 134)} = 0.149$, $p = 0.637$, Figure 4.7B) nor the reproductive success (Simple Regression: $R^2 = 0.014$, $F_{(1, 130)} = 0.1.847$, $p = 0.176$). The visiting frequency did as well not show any influence on the plants' fruit set (Simple Regression: $R^2 = 0.002$, $F_{(1, 134)} = 0.027$, $p = 0.778$, Figure 4.7C), seed set (Simple Regression: $R^2 = 0.025$, $F_{(1, 130)} = 3.332$, $p = 0.375$, Figure 4.7D) nor reproductive success (Simple Regression: $R^2 = 0.008$, $F_{(1, 130)} = 1.007$, $p = 0.318$). Focusing on the honey bee *Apis mellifera*, which is the most-effective as well as most abundant pollinator, the abundance did not have any influence on fruit set and reproductive success as well. I found a marginal influence on the seed set of *J. flava* (Table 4.5).

Backwards multiple regressions were conducted to investigate the influence of a number of factors on the fruit and seed set. Concerning the fruit set of *J. flava* the combination of the factors: number of *J. flava* flowers, cloud cover, wind speed, number of plant species and distance to forest showed the highest influence (R^2 = 0.392, F(5, 108) = 13.908, p < 0.001; started with n = 12 factors). The beta coefficients are presented in Table 6. The factors soil pH, canopy cover, visit duration and the numbers of flowers of other plants, of bee species and visits did not show a significant influence and were excluded from analysis.

Investigating the seed set, the results were significant when the factors: duration of flower visit, number of *J. flava* flowers and distance to forest were included (R^2 = 0.177, F(3, 110) = 7.905, p < 0.001). The beta coefficients are presented in Table 4.7. Note that number of *J. flava* flowers and distance to forest predicted the number of seeds (on a low level) when also the flower visitation duration was included, which by itself did not have a significant influence on the seed set. The factors soil-pH, canopy and cloud cover, windspeed, numbers of bee species, flowers of other plants, flower visits, and plant species were excluded.

Concerning the reproductive success the combination of number of *J. flava* flowers, cloud cover, windspeed, number of plant species per plot and distance to the forest showed the highest influence (R^2 = 0.313, F(5, 108) = 9.844, p < 0.001) (Table 4.6). The beta coefficients are presented in Table 4.8. The factors soil-pH, number of flower visits and of flower visiting species were excluded.

Table 4.5:
Influence of the abundance of flower visiting honeybees on (A) fruit set (R^2 = 0.00, $F_{(1,134)}$ = 0.018, p = 0.894), (B) seed set (R^2 = 0.027, $F_{(1,130)}$ = 3.66, p = 0.058), (C) reproductive success (R^2 = 0.007, $F_{(1,130)}$ = 0.967, p = 0.327 of *Justicia flava*; simple regression analysis

Variable	B	SEB	β	p
(A) Fruit set				
No. of honeybee visits (sqrt.)	0.004	0.032	0.011	0.894
(B) Seed set				
No. of honeybee visits (sqrt.)	0.142	0.074	0.166	0.058
(C) Reproductive success				
No. of honeybee visits (sqrt.)	0.094	0.096	0.086	0.327

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

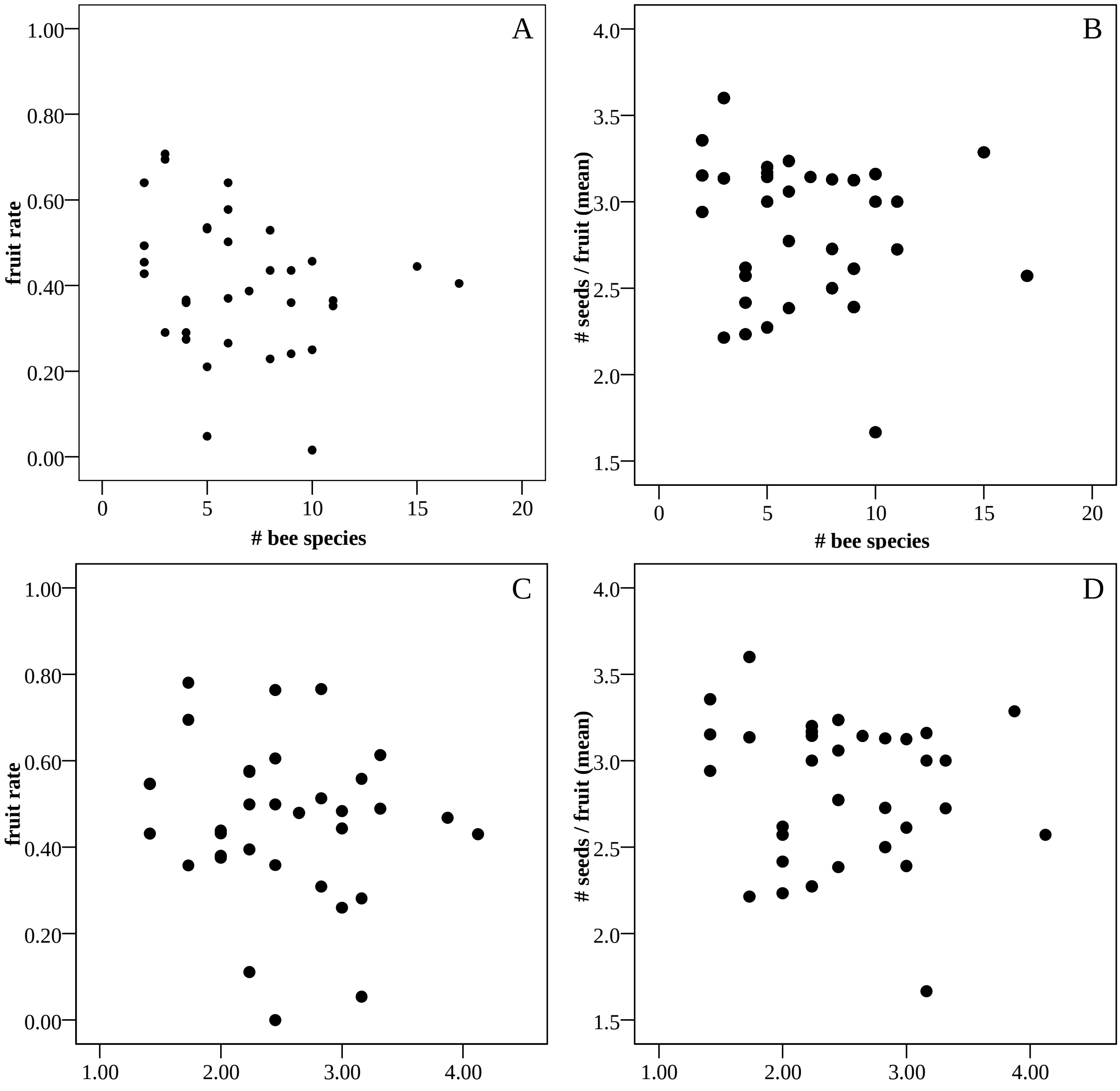

Figure 4.7:

Fruit and seed set of *Justicia flava* in relation to species number and abundance of bees in the 35 study sites. (A) fruit set as a function of bee species richness; (B) seed set as a function of bee species richness; (C) fruit set as a function of bee abundance; (D) seed set as a function of bee abundance

Table 4.6:

Factors influencing the fruit set of *Justicia flava*. Final model coefficients of a backward multiple regression ($R^2 = 0.392$, $F_{(5,108)} = 13.908$, $p < 0.001$; started with N = 12 factors). Dependent variable: fruit rate (sqr-transformed).

Variable	B	SEB	β	p
no. *J.flava* flowers (sqrt.)	0.478	0.091	0.475	< 0.001
cloud cover	0.038	0.014	0.206	0.007
canopy cover	0.082	0.017	0.368	< 0.001
no. plant species / site	0.005	0.001	0.469	< 0.001
distance to forest	-0.0000116	0.000003	-0.358	< 0.001

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

Table 4.7:

Factors influencing the seed set of *Justicia flava*. Final model coefficients of a backward multiple regression ($R^2 = 0.177$, $F_{(3,110)} = 7.905$, $p < 0.001$; started with N = 12 factors). Dependent variable: number of seeds/fruit (mean).

Variable	B	SEB	β	p
duration of flower visit (mean)	0.006	0.003	0.160	0.073
no. *J. flava* flowers (sqrt.)	0.770	0.238	0.288	0.002
distance to forest	-0.000028	0.000008	-0.324	< 0.001

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

Table 4.8:

Factors influencing the reproductive success of *Justicia flava*. Final model coefficients of a backward multiple regression (R2 = 0.313, $F_{(5,108)} = 9.844$, $p < 0.001$) Dependent variable: reproductive success (fruit rate x seed rate)

Variable	B	SEB	β	p
no. *J.flava* flowers (sqrt.)	1.453	0.319	0.438	< 0.001
cloud cover	0.101	0.049	0.166	0.04
wind speed	0.215	0.059	0.292	< 0.001
no. plant species / site	0.010	0.003	0.303	< 0.001
distance to forest	0.000	0.000	-0.407	< 0.001

B = regression coefficient; SEB = standard error of B, β = standardized beta coefficient.

4.5 Discussion

In this study, the flowers of Justicia flava were found to be visited by a large number of bees and some other insects. However, the composition of the flower visitors differed highly between study sites (2 to 19 species) as well as habitat types (29 species at the forest edge to 43 species in the farmland). While the highest number of bee species was found in the farmland, the visitor community in this habitat type was highly dominated by the honey bee *Apis mellifera*, which made up to 68% of the flower visits. The species richness inside the forest was slightly smaller (40 species compared to 43 species), but no dominant species could be identified and the composition of flower visitors showed a high eveness, as indicated by the shape of the Rényi Diversity Profiles (Figure 4.4). Thus, flower visitor diversity, which is composed of species richness as well as eveness, is highest inside the forest. The flower visitor community of *Justicia flava* at the forest edge was relatively poor, and extremely dominated by the honey bee. The high dominance of honey bees outside the forest can be explained by the circumstance that the farmland holds a relatively high number of beehives and natural nests as well, which are harvested regularly by local people for private as well as commercial purposes. Inside the forest, honeybees were very rare, even though some few natural nests were found as well. Flowers of *Justicia flava* can be found throughout the year, and are thus a reliable and highly attractive nectar source for the visiting bees. Especially if the plant occurs with large flower displays it is highly attractive for eusocial bees (like the honey bee), which need high amounts of nectar and pollen to provide their colonies with food. The honey bees showed aggressive behaviour at the flowers, and I observed some signs of competition between them and the solitary bees.

The tendency was found, that the diversity of bees visiting the flowers of *J. flava* decreased with increasing distance to the forest. This pattern was true up to a distance of about 1500m, while no tendency was observed farther away from the forest. This tendency indicates the different importance of *Justicia flava* as food source in the habitat types. As long as there are no mass-flowering trees inside the forest, bees rely on very few flowering plant species. *J. flava*, which flowers almost throughout the year, is one of the most important food sources in this habitat. Especially during the observations, I hardly observed other flowering plant species. Outside the forest, several plant species flowered, and bees were not depending on one single food source as inside the forest. With an increasing number of different flowering plant species, the diversity of bees visiting *J. flava* decreased.

At the forest edge, a lot of honey bees visited the flowers of *J. flava* very frequently. Conceivably, they competed with other flower visitors for nectar. Individuals of other bee species might have switched to other floral resources to avoid this resource sharing, respectively competition. Farther from the forest, no such effect could be found, and the differences in bee species composition were caused by other factors, like habitat quality and landscape structure.

Diversity as well as abundance of bees increased with the increasing flower display of *J. flava*, and decreased with increasing canopy cover and flower display of other plant species. Interestingly, a correlation between diversity and abundance was found. This is caused by the composition of the flower visitors as I found only one or two specimens of many species in the whole observation period.

Numerous studies showed that various pollinators, especially social bees can assess the costs and rewards of floral choices, and their visitation can be highly sensitive to resource density and dispersion (WADDINGTON & HEINRICH 1981, REAL 1981, REAL ET AL. 1982). In dense floral patches of *J. flava*, social bees tended to visit more flowers than in sparse patches. My results suggest and conform to the findings of other authors, that the size of a plant population respectively the size of its flower display has a positive effect on the visitation frequency of pollinators (HEINRICH 1979, WADDINGTON & HEINRICH 1981, ROUBIK 1982, REAL 1983, KIRCHNER 2005) as well as on the pollination success (e.g. KUNIN 1993, AIZEN & FEINSINGER 1994). Not only the number of conspecific flowers but also the number of flowers belonging to other plant species can influence pollination systems as we could show in this study. While a number of studies support the facilitative effect of shared flower displays because of the conjoined attraction to pollinators (THOMSON 1978, BROWN & KODRIC-BROWN 1979, RATHCKE 1983, GHAZOUL 2006), I found signs for competition in the present system. The number and abundance of insects visiting *J. flava* flowers was negatively correlated to the overall flower display. Due to the high attractiveness of *J. flava* to flower visitors it might have acted as a magnet species especially inside the forest (THOMSON 1978, LAVERTY 1992, JOHNSON ET AL. 1993). The magnet species, as its name implies, increases the local abundance of pollinators and thus appear facilitative for neighbouring plants with inferior rewards. Furthermore, the flower visitors of *J. flava* were negatively influenced by the weather conditions and the number of bees decreased with increasing cloud cover, showing the dependency on dry and sunny weather.

Justicia flava is a self-incompatible plant species, which obligatorily relies on the pollination by bees. Due to the fact, that the flowers provide nectar to their visitors, they are not only a food source for female bees, which collect pollen and nectar for provisioning their brood cells. They are also very important for male and parasitic bees, which collect nectar to maintain their own energy requirements only.

Several studies showed the positive influence of pollinators' abundance on the reproductive success of plants (KUNIN 1993, LARSON ET AL. 1999, HERRERA 2000, MORANDIN ET AL. 2005), while few studies also found a direct influence of pollinator diversity on the reproductive success of highland coffee (*Coffea arabica*, KLEIN ET AL. 2003) and watermelon (*Citrullus lanatus*, KREMEN ET AL. 2002). Seed and fruit set of the self-incompatible *Justicia flava* varied between study sites and habitats. However, the pollination system of *J. flava* was neither positively nor negatively influenced by the abundance and diversity of its entire flower visitor community although bee species differed in their ability to pollinate *J. flava* flowers. The flower visiting frequency on the study sites was very high, varying between one and fourteen visits per hour. The number of pollen grains, deposited on the stigmas should have been large enough, to induce full fruit and seed set, even on the study sites with low visitation frequency. Studies on other plant species showed, that fruit set can occur at pollination intensities of single pollen per ovule or even less (e.g. BERTIN (1982) on *Campsis radicans* (Bignoniaceae), SNOW (1982) on *Passiflora vitifolia* (Passifloraceae), MC DADE (1983) on *Trichanthera gigantea* (Acanthaceae)).

Although the flowers of *J. flava* are dichogamic (male and female phase are separated in time, LLOYD & WEBB 1986), which is described as one of the mechanisms preventing self-pollination, the dichogamy found is not synchronous within a plant. Thus, neighbour pollination is possible, but, as highlighted before, resulted in a lower seed set. This pattern was also found in other plant species (STEPHENSON 1981). The honeybee *Apis mellifera* was the most efficient pollinator of *J. flava*, as well qualitatively, revealed by single-visit experiments, as quantitatively due to its high abundance especially in patches with large flower displays. As a single honey bee-visit to a virgin flower on average resulted in almost 75% seed set (2.87 out of 4 possible seeds), the reproductive effect of surplus visitation was rather low. Due to relatively high visitation rates, pollination limitation was not observed. To assess the different influences of the very dominant honey bee on one side and the solitary bees on the other hand I analysed the data for these two groups separately. While I did not find any effect of the abundance of the honeybees on the fruit set of *J. flava*, the seed set was (marginally significantly) positively influenced by their abundance. The observed effect was rather low, but showed the different responses of fruit and seed development to factors.

Focusing on the solitary bees, no significant effects were observed and fruit and seed set were independent of the diversity and abundance of the solitary bees.

However, the reproductive success of *J. flava* did not reach 100%. Besides the limitation by the pollinator behaviour, several other parameters can cause limitations, like the quality and quantity of pollen, inbreeding depression, resource limitation, or coevolutionary adaptations or strategies of the plants (KUNIN 1997, ROLL ET AL. 1997, BOSCH & WASER 2001, ASHMAN ET AL. 2004). Fruit and seed set of *J. flava* were both positively influenced by the number of conspecific flowers in the neighbourhood. A high number of flowers is directly correlated to a high number of pollen, which could potentially be deposited on the stigmas. Furthermore, a high number of flowering plants could imply that the proportion of geitonogamous pollination might be rather low, if genetic diversity is still high. While the seed set was only marginally influenced by the distance to the forest and marginally and insignificantly by the visit-duration of the pollinators, the fruit set was (highly) influenced by abiotic and habitat factors, like cloud and canopy cover and the number of plant species on the study sites. Dense cloud and canopy covers cause high humidity and low temperature values. Especially in very humid areas, like the Kakamega Forest, these factors can increase the proportion of fruits going mouldy. Furthermore, resource limitation of fruit production can be the result of inadequate soil nutrients, water, or light (e.g. CARUSO ET AL. 2005) and as this study was conducted in an extremely marked dry season, water could have acted as the resource-limiting factor.

This study was carried out in natural populations. Thus, the uncontrolled and unmeasured environmental and genetic (inbreeding depression) factors possibly affected and overlaid the measured effects. While 39% of the variance in fruit set was explained by the above mentioned factors, the (co-)evolutionary background can explain a fraction as well. E.g. hermaphroditic plants commonly produce more flowers than are matured into fruit, resulting in fruit-to-flower ratios less than unity (STEPHENSON 1981, SUTHERLAND & DELPH 1984, HOLLAND ET AL. 2004). Studies showed, that the production of surplus flowers is advantageous because it increases the male contribution to fitness (pollen donation), rather than the female contribution (seed production) (WILLSON & RATHCKE 1974, WILLSON & PRICE 1977, STEPHENSON 1981). This pattern might be true for *J. flava* as well.

Even if diversity and abundance of pollinators did not show any direct influence on the fruit and seed set of *J. flava* in this short-term observation, the composition of visitor and also plant communities are of great importance for the long term preservation of maintenance of plant pollinator systems. Floral abundance in species, even in perennial communities can vary highly among years (reviewed by Tepedino & Stanton 1980, Rathcke 1983) and in space (Lazaro & Traveset 2005, de la Bandera & Traveset 2006). Nectar production, for example, can vary with rainfall or insolation within a species (Feinsinger et al. 1979). Because local populations are open systems, pollinator limitation may alternate with overabundance in different sites and years, lending unpredictability to interactions and their outcomes. Furthermore, in some study areas the number of flowers of *J. flava* and their density reached high values. Pollinators may become more sedentary and even territorial (Feinsinger 1976, Stephenson 1982), and most visits may be local. This and the high portion of honeybees in the visitor community have the potential to increase improper pollen transfer if visits occur mainly within one individual plant or among closely related plants (Price & Waser 1979, Augspurger 1980, Stephenson 1982). *Apis mellifera*, the most important pollinator of *J. flava* collects, like all social bee species, big amounts of nectar and pollen for brood provisioning very economically through successive visits to several flowers on each plant (e.g. Galen et al. 1985, Visscher & Seeley 1982, Seeley 1985). Although Thomson & Plowright (1980) showed that a bee load of pollen may be deposited over up to seven sequential flower visits, actual pollen carryover from outcross flowers seems to be lower than this, because bee loads are accumulated from geitonogamous pollen and also from several pollen sources. Thus geitonogamy is bound to occur in *J. flava*, except for the rare situation when pollinators visit only a single flower per plant during a foraging bout. The influence of paternity on realized reproductive output cannot be ruled out (Herrera 1987), as the seed set of *J. flava* was smaller after geitonogamous pollination and as previous studies have often shown greater survival of seedlings from crossed versus inbred or selfed progeny (Price & Waser 1979, Hessing 1988, Finer & Morgan 2003, Young et al. 1996, Armbruster & Rogers 2004, Hirayama et al. 2005).

Not to suffer from inbreeding, *J. flava* is reliant on either (long-distance) cross pollination or seed dispersal. Explosive seed dispersal, like in *J. flava* is a short-distance process, distributing the seeds most likely in a distance below 6 meters away from the mother plant (Stamp & Lucas 1983, Garrison et al. 2000). Secondary dispersal by ungulates (at least inside the forest and at the forest edge) which feed on grass and herbs might be possible. They distribute the seeds endozoochorically or exozoochorically in their fur (Kiviniemi 1996, Mouissie et al. 2005, Howe & Miriti 2004) even if the seeds do not have any hooks or sticky substances on the surface (Fischer et al. 1996). The plant’s life cycle is embedded in an ecological context in which many hazards may affect from one to several different stages of the process by operating through certain phenotypic traits of the plant. The effect of pollinators on total fitness can be weakened through other factors accounting for a greater effect on the plant's fitness (HERRERA 1996).

Justicia flava is a highly successful plant with a generalized pollination system, which is a typical phenomenon in tropical regions due to the high spatiotemporal variability in the composition of the floral visitor assemblage (GÓMEZ & ZAMORRA 2006). The self-incompatible flowers, which rely on bee-pollination, seem to be an important food source for large numbers of visiting bees and butterflies, especially inside the Kakamega Forest. Since this very common plant species is found in several different habitats in tropical Africa, populations of *J. flava* might serve as stepping stones for flower visitors in areas with spatiotemporal habitat changes, where only small amounts of other food sources are accessible. GIKUNGU (2006) highlighted the importance of *J. flava* to several species of bees inside Kakamega Forest. However, the attractiveness of *J. flava* seems to work as a magnet for flower visitors (THOMSON 1978, JOHNSON ET AL. 2003) and thus might facilitate the reproductive success of relatively rare co-flowering plants.

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5. SMALL-SCALE HETEROGENEITY IN FLOWER VISITOR COMMUNITIES OF *JUSTICIA FLAVA* (ACANTHACEAE) IN AGROECOSYSTEMS OF KAKAMEGA, WESTERN KENYA

5.1 Abstract

Bees usually have a rather small foraging range (solitary bees: 150 m – 600 m, African honeybees: 400m - 1000m), although reports about foraging distances up to several kilometres can be found. Thus, local habitat structure and resource configuration appear of great importance to the behaviour of bees. In this study I investigate the small spatial scale differences in uniform habitats (3 habitat types: farmland, forest edge, forest interior) of the flower visitor species of *Justicia flava* (Acanthaceae), an entomophilous herb, common to Eastern Africa. Comparative results show, that the composition of flower visitors did not only differ clearly between different habitats, but also between study sites, closely located in the same habitat type (distance between 200 m - 2000 m). In total *J. flava* is visited by a large variety of bees (66 species), but only by 3 - 19 species at a single site. Values for the Morisita-Horn Similarity Index varied obviously (within habitat types between S = 0.00 and S = 0.59) and spatial distance had a high significant effect on the composition of flower visitors. Especially in the farmland as well as inside the forest the effect was pronounced, while the effect was not found between study sites located at the forest edge. Thus, bee species composition, especially in forested areas with small numbers of flowers seems to be spatially heterogeneous and thus difficult to predict.

As geographic differences in interactions are an inherent part of the coevolutionary process, and geographically structured species tend to coevolve towards a complex spatial mosaic of coevolutionary hot spots and cold spots, there is the potential of coevolutionary shifts in the pollination system of *Justicia flava*.

5.2 Introduction

In nature, organisms are distributed neither uniformly nor at random. Rather, they are aggregated in patches, or they form gradients or other kinds of spatial structures. Although the spatial heterogeneity of populations and communities plays a central role in ecological theory (Legendre & Fortin 1989), relatively little attention has been given to variation over time and space in flower visitor or pollinator faunas, especially at intermediate spatial scales and within more or less homogeneous habitats (but see Herrera 1988, Horvitz & Schemske 1990, Fishbein & Venable 1995). However, the evolution of species interactions can only be fully understood by considering their variation in space and time (Thompson & Pellmyr 1992, Brody 1997, Gomez & Zamora 2000), because this variation can limit species responses to selection (Rey et al. 2006). Spatial or geographic variation forms the basis of the geographic mosaic theory of coevolution (Thompson 1997, 1999), which suggests that much of the dynamics of coevolution between pairs or groups of species often occurs at a geographic scale above the level of local populations and below the level of the fixed traits of interacting species (Thompson 1997).

According to Ashmann et al. (2004), variation in pollinator composition and pollination service has the potential to profoundly influence the ecological dynamics of plant populations and communities. But, little is known about variation in pollinator composition and pollination service to single plant species (Price et al. 2005). Spatial variation in pollinators is the logical consequence of well-known, widespread phenomena such as microclimatic preferences related to physiological tolerance (Taylor 1963, Rawlins 1980, Chappell 1982), and habitat selection (Erhardt 1985), or requirements in terms of nesting sites versus foraging sites (Tscharntke et al. 1998, Gathmann & Tscharntke 2002). In the case of a plant species that interacts mutualistically with animals for pollination or seed dispersal, one of the most obvious potential causes of unpredictability in selective pressures is variation in time or space of the assemblage of its animal mutualists. Especially in “year-long” systems, like in tropical rainforests, pollinator and plant abundance are not only likely to fluctuate across years, but also across seasons (Medan et al. 2006). Thus, tropical mutualistic interactions involving an assemblage of species are far more frequent than one-on-one mutualisms or taxon-specific coevolution (Horvitz & Schemske 1990, Waser et al. 1996, overview in Waser & Ollerton 2006). However, the tropics do appear to have a greater range in degree of specialization than temperate zones, as the number of functional groups of pollinators declines with latitude (bird or bat pollination is only possible in areas where these animals visit flowers) (ARMBRUSTER 2006).

Individuals or populations of plant species that occur in a variety of different habitat types might show different phenological characteristics due to differences in environmental parameters like solar irradiation, humidity, soils etc. Concerning flowering phenology, GENTRY (1974) described the endpoints of the broad spectrum as the “steady state” and the “big bang”. While the latter describes mass flowering phenomena, which occur mainly outside the forest or in the forest canopy, the “steady state” bloomers, which are found frequently in the forest understory communities (KATO ET AL. 2005), depend for pollination on the fixed foraging patterns of pollinators, designated “trap liners” by JANZEN (1971), which visit flowering plants as part of a standard sequence, after having learned the location of a particular plant. Once incorporated on a trapline, such a plant enjoys a higher frequency of pollinator visits per unit of energy expended and a greater likelihood of cross pollination. Trap-lining has been reported in several bumblebee species, euglossine bees, honeybees, but also hummingbirds, tamarins, rats, pied wagtails and long-nosed bats (see SALEH & CHITTKA 2007 for references). On the opposite, the “big bang” blooming is especially highly interesting for social bees and their high energy needs due to large colony sizes and the year-through activity patterns.

In this study, I investigated the similarity or dissimilarity in flower visitor composition of the common entomophilous herb *Justicia flava* (Acanthaceae) within and between habitats. I also investigated the role of spatial correlation between flower visitor compositions as a base to understand the spatial organization of pollinator communities. As an indirect measure of behaviour, I predicted that pollinator composition should be dissimilar between different habitat types, and more similar between study sites belonging to the same habitat type, due to similar environmental parameters like irradiation, humidity and food sources. Within homogeneous zones, biotic processes often produce an aggregation of organisms, following various spatiotemporal scales, which can be measured (LEGENDRE ET AL. 1985). Typically, locations that are close together tend to have more similar values, or are more positively correlated, than those that are farther apart; this tendency is termed spatial autocorrelation (LEGENDRE & FORTIN 1989, VER HOEF & CRESSIE 2001). Thus, I expected spatial autocorrelation to be positive for short distances among points.

5.3 Material and methods

5.3.1 Study area and study sites

Study area was the Kakamega Forest, a tropical rain forest remnant and it's surrounding agricultural areas. The forest is located in western Kenya (0°17'N, 34°54'E) at an altitude of 1,500 m to 1,700 m, about 50 km north of Lake Victoria.

The study was conducted in 15 study sites located inside and around the northern part of Kakamega Forest in the three different habitat types farmland, forest edge and forest interior, with five replicate plots in each habitat type (Figure 5.1).

The study sites were ten by ten metres square, and in close vicinity to each other. Study sites of the same habitat type were not farther than 2,800 metres from each other (Appendix 1), while the farthest distance between study sites of different habitat was 4,500 metres, that was, between Kabrasi B in the farmland and Salazar B in the forest.

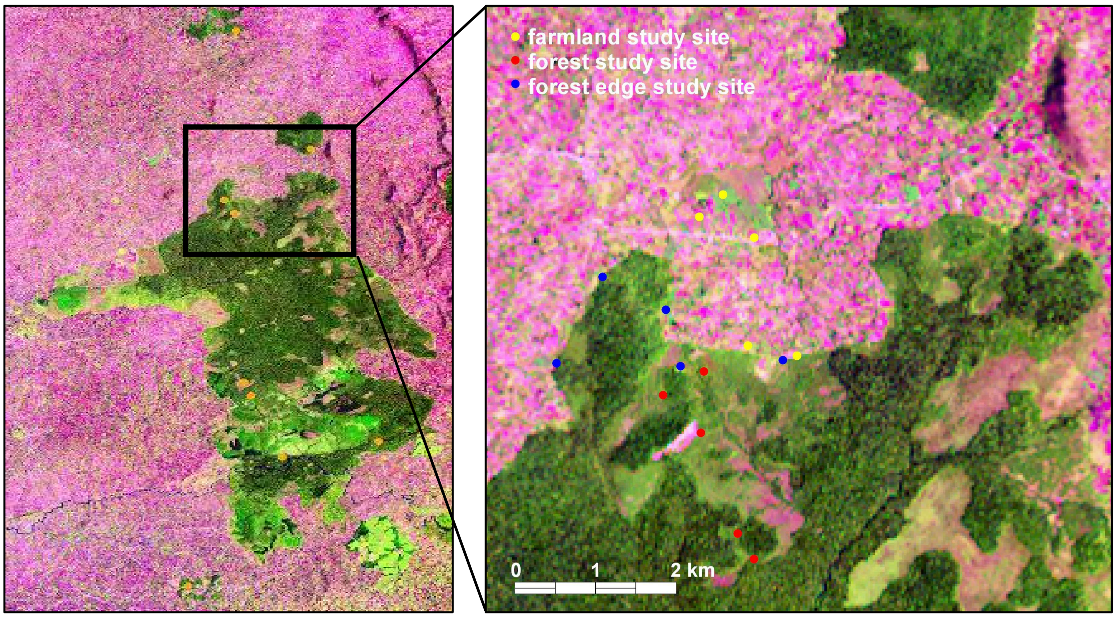

Figure 5.1:
(A) Satellite image of Kakamega Forest and the surrounding farmland (Landsat ETM + (7); 05 Feb 2001, spectral bands 5/4/3, contrast enhanced);
(B) Detail: the study area in the northern part of the forest.
courtesy of G. Schaab

Plant communities

In the beginning of the study, the vegetation in the study sites was identified and mapped. The cover of canopy, giving shade to the herbal layer and thus the focal plant, was estimated using a percentage scale (from 0% = no canopy to 100% = complete canopy coverage). This canopy cover in each study site was used for analysing potential influence of the canopy cover on the visitation frequency.

Parallel to the flower visitor observation units I conducted flower counts to produce a quantitative measure of flower density of *Justicia flava* and all other plant species at each study site.

5.3.2 Flower visitor composition

Flower visitors of Justicia flava

The monitoring of the composition of flower visitors of *J. flava* was done between January and February 2005. Five observation units were conducted on each of the 15 study sites. Flower visitors were observed in 30-min units between 10.00 am and 02.00 pm on sunny days. In these observation units ten flowers were observed, every visitor, the number of flowers it visited, and the flower visit duration recorded. These data provided a basis for the calculations of species composition, the abundance and diversity of the flower visitors. After each observation unit conspecific and heterospecific flowers were counted, and flower visitors were caught with a sweep net for 10 minutes for later identification. It was not possible, to identify some of the small visitors up to species level in the field, due to their size and colour. In order to avoid interfering with the flower visiting behaviour of the bees, small bees were grouped in 4 groups (Appendix 5.2).

Diversity and similarity

The within-habitat-diversity of flower visitors was calculated using the Rényi diversity index (Rényi 1961, Tóthmérész 1995).

$$H_\alpha = \frac{\ln\left(\sum_{i=1}^{s} p_i^\alpha\right)}{1-\alpha}$$

H_α = Rényi Diversity Index
p_i = proportions of each species
α = scale parameter

A profile is calculated by changing the value of α from 0 to infinity. In this thesis the values of α are: 0, 0.25, 0.5, 1, 2, 4, 8, 16, Inf. (vegan package, Oksanen et al. 2006). The shape of the Rényi-curve profile is an indication of the eveness. A horizontal profile indicates that all species have the same eveness. The less horizontal a profile is, the less evenly species are distributed. If the profile for one site is everywhere above the profile for another site, then this means that the site with the highest profile is the more diverse of the two. If the profiles intersect, it is not possible to order the sites from lowest to highest diversity (KINDT & COE 2005).

The similarity of flower visitor compositions between the different study sites was investigated using Morisita-Horn Similarity measurements (MORISITA 1959, HORN 1966). This index measures similarity between two communities and varies from 0 (no similarity) to about 1.0 (complete similarity). The index is nearly independent of sample size and compares abundances, species by species (CHAO ET AL. 2005).

$$C_H = \frac{2\sum X_{ij} X_{ik}}{\left[\left(\sum x_{ij}^2 / N_j^2\right) + \left(\sum x_{ik}^2 / N_k^2\right)\right] N_j N_k}$$

C_H = Morisita-Horn Index of similarity between sample j and k
X_{ij}, X_{ik} = number of individuals of species i in sample j and sample k
$N_j = \Sigma X_{ij}$ = total number of individuals in sample j
$N_k = \Sigma X_{ik}$ = total number of individuals in sample k

5.3.3 Spatial autocorrelation

The Mantel Test was conducted to investigate the influence of geographical distance on the bee composition in the different study sites. The test is based on distance matrices and permutation tests and examines the relationship between two matrices (MANTEL 1967). The Mantel Test computes a correlation between the two n x n distance matrices, where one matrix might represent spatial distances for example, whereas the other represents differences (= distances) between ecological variables or patterns (e.g. bee species composition). In calculating the Mantel statistic, the products of corresponding elements of the distance matrices (A_{ij} and B_{ij}) summed as follows for $i \neq j$:

$$Z = \sum_{i=1}^{n} \sum_{j=1}^{n} A_{ij} B_{ij}$$

Z = Mantel coefficient
A = variable distance matrix (here: Morisita-Horn Dissimilarity of bees)
B = actual Euclidean (spatial) distances among the n study sites

For preparing distance matrices, the Morisita-Horn Dissimilarity (1- M-H Similarity) was calculated between the bee communities of the different study sites, and Euclidean Distance was calculated for the geographical distance as well as for the differences in flower number between study sites. To overcome the problem of unbounded Z-statistic, which can not be compared from one study to another, the Z-statistic can be normalized (r) such that it behaves as a product-moment correlation coefficient (similar to Pearson's r representing a linear relationship), which ranges from -1 to +1. The normalization of each distance matrix was carried out separately using the standard normal transformation, subtracting the mean of that matrix from each element, and then dividing by the standard deviation of the elements in that matrix. This normalized Mantel statistic (r) can be used to compare results from different variables, or studies, by means of confidence limits, as described by MANLY (1986, 1997). When the r-statistic is calculated between a variable distance matrix and a geographical distance matrix, the value of r corresponds to the average magnitude of spatial autocorrelation of the variable for the entire study area. Because the Mantel statistic cannot be tested as an ordinary product-moment correlation because the distances in each matrix are not independent of one another, the significance is assessed by using a permutation test to construct a reference distribution. In this permutation test, the statistic calculated on the actual data is compared with what happens when the elements of the matrices are shuffled at random. If there is a strong spatial pattern in the data, shuffling the data points will eliminate that pattern. In this project, the number of permutations was 5000.

Space can create spurious relations between two variables that are in fact driven by a spatial gradient or by a third variable that follows the spatial gradient. To address this issue, partial Mantel test allows the comparison among three distance matrices. A partial correlation between two matrices is calculated, keeping the effects of the third matrix constant. The test was conducted to investigate the influence of food availability on the bee composition in the different study sites. Partial Mantel Test was conducted, with the Morisita Horn Dissimilarities building the first cross table, the geographical distance building the second and the differences in flower numbers building the third cross table.

5.3.4 Data analysis and statistics

In this study the received data were listed with Microsoft Office Excel 2003. Rényi diversity profiles were produced, and Morisita-Horn Similarity, Euclidean distances and Mantel Test calculated using R 2.4 (The R Development Core Team 2006) and the R package vegan 1.8-3 (OKSANEN ET AL. 2006).

A result is called significant, if the significance level is $p \leq 0.05$, highly significant, if the level is $p \leq 0.001$ and marginally significant, if $0.10 \leq p \leq 0.05$.

5.3.5 Identification of bees

Identifications of the flower visiting bees were done by two specialist taxonomists for African bees. Dr. Mary Gikungu (National Museums of Kenya, Nairobi) worked on the families Megachilidae and Halictidae, and Dr. Connal Eardley (Plant Protection Research Institute, Pretoria, South Africa) identified the specimens belonging to the Apidae.

5.4 Results

5.4.1 Flower visitor composition and diversity

During the study 2264 visits of 64 species of bees were recorded on the flowers of *Justicia flava* (Appendix 5.2). The highest species richness was found inside the forest (total: 47 species, Salazar A: 19 species, Table 5.1), while highest abundance was observed in the farmland. The most abundant species was the honey bee *Apis mellifera*, which was responsible for 71% of the total flower visits and thus highly dominant.

Table 5.1:
Number of flower visitor species and their visits to *Justicia flava*

habitat type	study site	number of visitor species	No. of flower visits by bees	No. of flower visits by *A. mellifera*	No. number of *J. flava* flowers (mean)
farmland	Buyangu C	8	281	205	197
farmland	Buyangu D	4	332	327	383
farmland	Kabrasi B	5	73	57	255
farmland	Kabrasi D	8	140	79	274
farmland	Kabrasi E	6	170	160	380
forest edge	Buyangu A	9	244	219	229
forest edge	Buyangu E	13	279	233	174
forest edge	Buyangu F	11	115	87	265
forest edge	Lusero B	9	121	98	512
forest edge	Upper Campsite	3	117	115	304
forest	Buyangu Hill	12	82	0	114
forest	Campsite A	9	64	8	77
forest	Mapera	15	105	34	69
forest	Salazar A	19	111	0	75
forest	Salazar B	12	29	1	15
	farmland	19	996	827	293
	forest edge	29	876	751	237
	forest interior	47	391	43	70
	total	64	2264	1622	249

Rényi diversity profiles showed not only the higher species richness but also higher evenness of the flower visitor composition inside the forest compared to the other two habitat types (Figure 5.2 A). In the different habitat types, the Rényi-profiles showed habitat-congruent shapes. While for all forest interior sites, the sparsely sloped Rényi profiles indicated high evenness (Figure 5.2 D), low evenness was found in the two habitat types outside the forest (Figure 5.2 B,C), displaying the high dominance of the honeybee *Apis mellifera*.

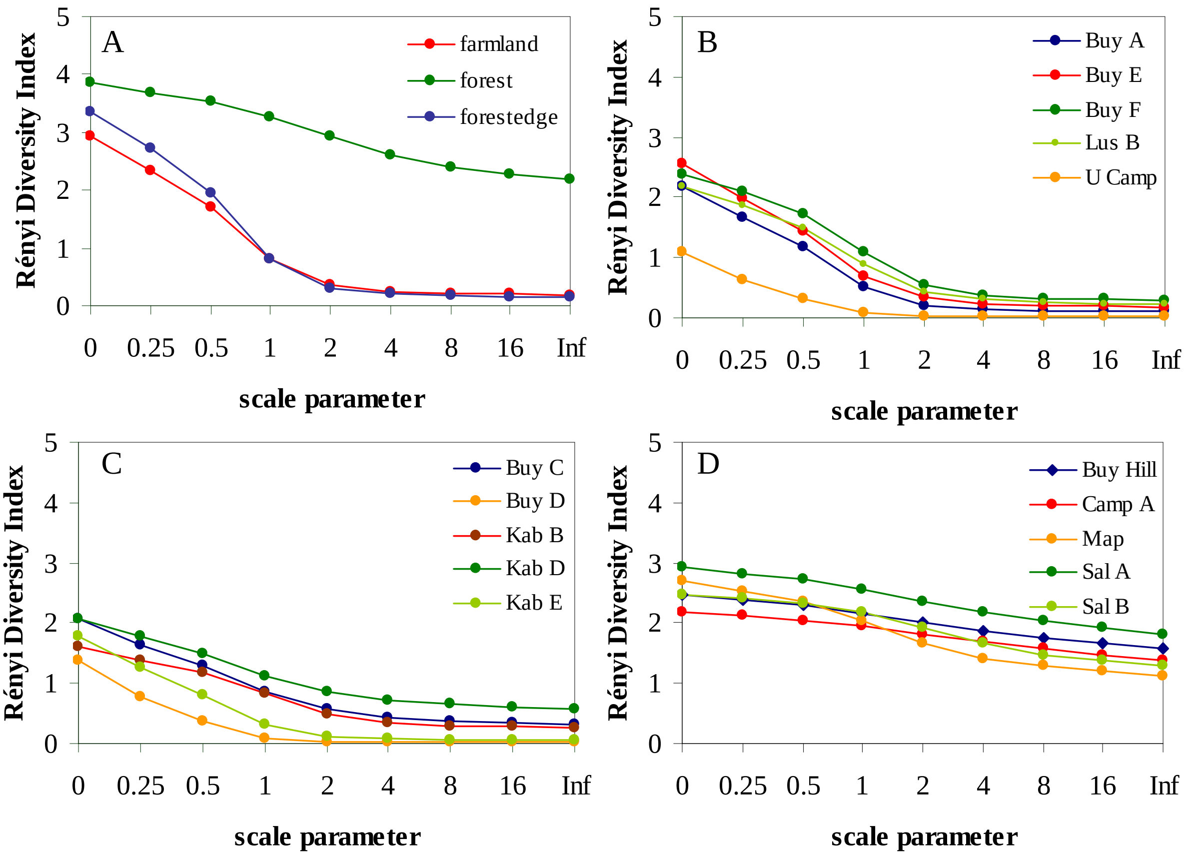

Figure 5.2:
Rényi Diversity Profiles of flower visiting insects of *J. flava*. A: Profiles of all visitors in the different habitats; B: Profiles of visitors in the different forest edge sites; C: Profiles of visitors in the different farmland sites; D: Profiles of visitors in the different forest sites.

5.4.2 Similarity in visitor composition between study sites

Morisita-Horn Similarity Index was calculated to compare the flower visitor compositions between the study sites of the same as well as of different habitat types.

Some species were found only on single study sites or in single habitat types. For example *Amegilla albigena* was found only in the farmland site Kabrasi D, while *Xylocopa calinata* was found only in the forest site Salazar B. *Xylomelissa* sp.1 occurred only inside the forest, and the males of *Xylocopa nigrita* were found only in the farmland study site Buyangu C, while the females were found only inside the forest. The case of *Xylocopa nigrita* might serve as an indication, that habitat specificity found in this study might be a result of under-sampling rather than real habitat specificity. Thus, absolute conclusions should be drawn cautiously. Only few species of flower visitors occurred on several of the study sites. The honey bee was found on 13 sites but was absent in Salazar A and Buyangu Hill while *Xylocopa calens* and *Xylocopa hottentotta* were found on only seven respectively five sites. Interestingly, *X. calens* was found only in open habitat types outside the forest, while *X. hottentotta* occurred only inside the forest and at the forest edge. Even if the number of flower visitors was not the highest at the forest edge, it was evident that this habitat shared quite a number of species with the other habitat types. Conversely, farmland and forest interior showed species, that did not occur in the completely different habitat types and the species seemed to be more or less habitat dependent.

Comparisons of the flower visitor communities between the different habitats showed, that the composition was rather similar between farmland and forest edge (overall: S = 0.99, for details see Table 5.2 A,B), while higher differences were found between both habitats compared with the forest interior (overall: S = 0.25 for both combinations).

Comparing the study sites within each habitat, Morisita-Horn Similarity measurements showed high similarity within either farmland and forest edge sites and low similarity within the forest (Table 5.2 A). In combination with the high species numbers inside the forest, this habitat type seemed to be highly diverse, inhomogeneous and difficult to predict. However, excluding *Apis mellifera* from the analysis changed the pattern, especially in the farmland and at the forest edge. In these two habitat types, similarities in bee composition between study sites decreased significantly, if only solitary bees were investigated (Table 5.2 B).

5.4.3 Spatial autocorrelation

Mantel Test was applied, to answer the question “Are samples that are close together also compositionally similar?”. The test was conducted with the Morisita-Horn Dissimilarities as dependent and the geographical distance as independent variable. However, while there was no spatial autocorrelation between visitor composition and geographical distance between the study sites at the forest edge (r = 0.003, p = 0.425), the effect was significant inside the forest r = 0.574, p = 0.026) and obvious but only marginally significant in the farmland (r = 0.72, p = 0.066) (Figure 5.3, Table 5.3). The same pattern appeared for the influence of geographic distance on the composition of solitary bees (excluding the dominant honeybee from analysis). While there was no effect at the forest edge, spatial autocorrelation was found in the other two habitat types (farmland: r = 0.448, p = 0.085; forest interior: r = 0.578, p = 0.01). Because of the honeybees' high dominance, the influence of geographic distance on the abundance of *Apis mellifera* was tested separately using Mantel Test. A strong correlation was found only among study sites in the farmland (r = 0.793, p = 0.008), while no spatial autocorrelation was found in the other two habitat types (Table 5.3). Partial Mantel Test was conducted to investigate the influence of the number of flowers on the flower visitor composition, but in farmland and forest edge no such effect was found. A marginally significant correlation was found inside the forest (r = 0.58, p = 0.072). However, inside the forest partial Mantel Test showed that correlation between the similarity Matrix and the geographic distance matrix increased significantly if the number of flowers was used as Z matrix (r = 0.575, p = 0.043). Geographic distance and flower number were themselves not correlated. This pattern was not found in the farmland and at the forest edge. During this study the forest was the only habitat where I found a correlation between geographical distance and flower number was found.

Table 5.2:
Morisita-Horn Similarities (A) of the flower visitor composition of *J. flava* between study sites of the same and of different habitat types; (B) of solitary bees visiting *J. flava* (*Apis mellifera* excluded)

A		Farmland					Forest Edge					Forest			
		BuyC	BuyD	KabB	KabD	KabE	BuyA	BuyE	BuyF	LusB	UCam	BuHi	CamA	Map	SalA
Farmland	BuyD	0.94													<0.25
	KabB	0.96	0.96											🟨	<0.50
	KabD	0.84	0.80	0.84										🟧	<0.75
	KabE	0.95	1.00	0.97	0.82									🟥	>0.75
Forest edge	BuyA	0.95	0.99	0.98	0.84	1.00									
	BuyE	0.98	0.98	0.98	0.84	0.99	0.99								
	BuyF	0.97	0.96	0.98	0.87	0.97	0.98	0.99							
	LusB	0.96	0.97	0.98	0.85	0.98	0.99	0.99	0.99						
	Ucam	0.94	1.00	0.96	0.80	1.00	0.99	0.98	0.96	0.97					
Forest	BuHi	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.04	0.02	0.00				
	CamA	0.25	0.22	0.25	0.26	0.22	0.24	0.24	0.27	0.26	0.22	0.07			
	Map	0.63	0.55	0.63	0.60	0.57	0.58	0.61	0.67	0.62	0.55	0.33	0.44		
	SalA	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.02	0.00	0.20	0.00	0.15	
	SalB	0.07	0.06	0.07	0.07	0.06	0.07	0.07	0.07	0.08	0.06	0.13	0.03	0.11	0.10

B		Farmland					Forest Edge					Forest			
		BuyC	BuyD	KabB	KabD	KabE	BuyA	BuyE	BuyF	LusB	UCamp	BuHil	CampA	Map	SalA
Farmland	BuyD	0.02													<0.25
	KabB	0.00	0.00											🟨	<0.50
	KabD	0.06	0.00	0.00										🟧	<0.75
	KabE	0.00	0.00	0.17	0.36									🟥	>0.75
Forest Edge	BuyA	0.00	0.00	0.09	0.63	0.26									
	BuyE	0.86	0.03	0.00	0.06	0.00	0.01								
	BuyF	0.29	0.00	0.00	0.25	0.09	0.44	0.41							
	LusB	0.00	0.00	0.00	0.15	0.03	0.22	0.01	0.26						
	Ucam	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00					
Forest	BuHi	0.00	0.00	0.02	0.03	0.04	0.12	0.06	0.39	0.27	0.00				
	CamA	0.00	0.03	0.00	0.03	0.00	0.18	0.00	0.18	0.10	0.00	0.07			
	Map	0.00	0.00	0.01	0.00	0.02	0.00	0.13	0.46	0.02	0.00	0.48	0.34		
	SalA	0.00	0.00	0.05	0.02	0.10	0.01	0.05	0.14	0.26	0.00	0.21	0.00	0.22	
	SalB	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.07	0.00	0.12	0.00	0.06	0.11

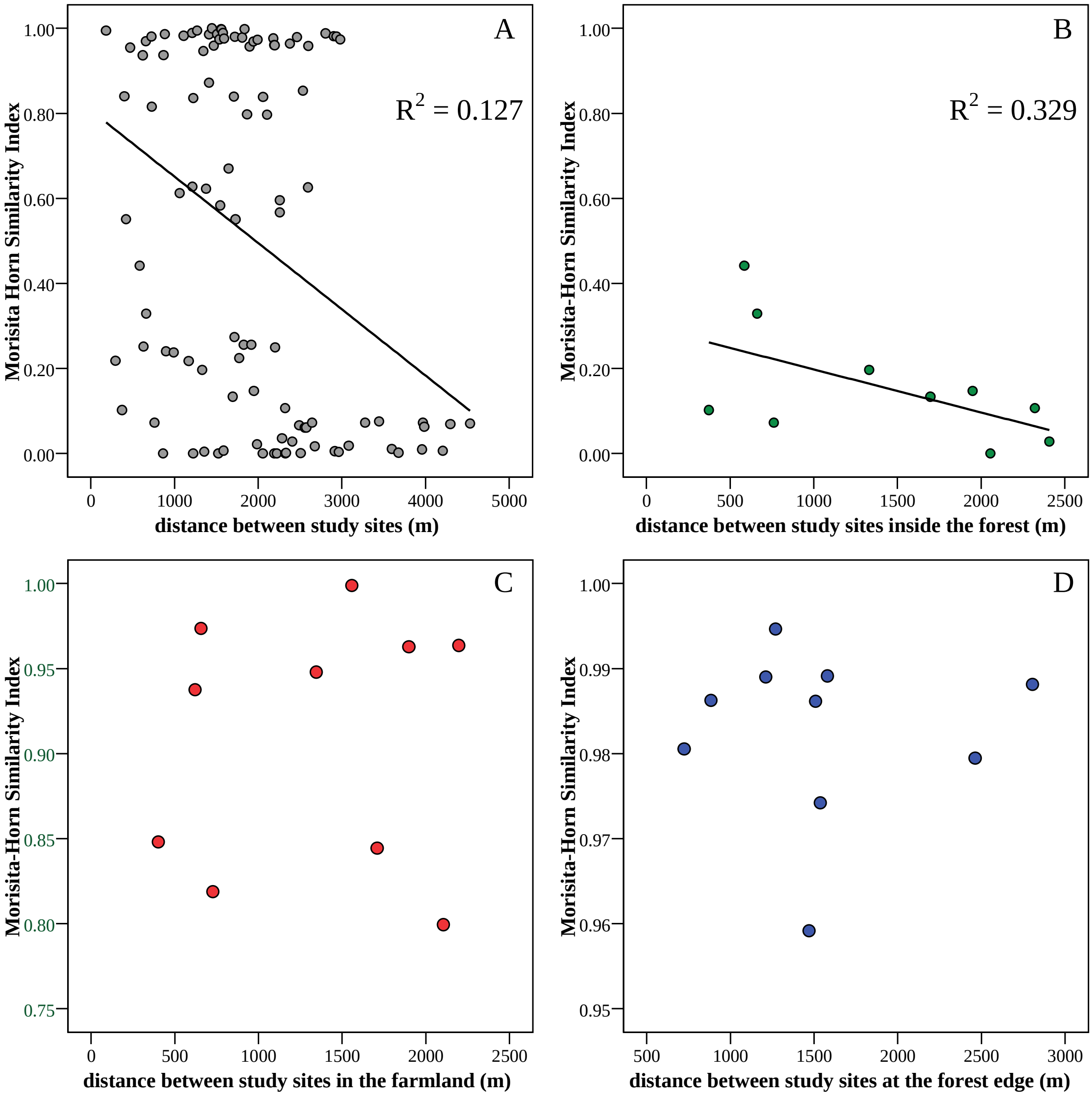

Figure 5.3:
Morisita-Horn Similarity Indices between study sites in relation to the distance between the sites. (A) all habitat types included, (B) forest sites only, (C) farmland sites only, (D) forest edge sites only. Significant spatial autocorrelation found only inside the forest (see Mantel Test).

Table 5.3:
Significant results of Mantel- and Partial Mantel test (simi= Morisita-Horn similarity of flower visitor group, flower= number of *J. flava* flowers, geogr.dist. = geographic distance between the study sites

					mantel-statistic	
visitor group	habitat type	x-matrix	y-matrix	z-matrix	r	p
all bees	farmland	simi	geogr.dist.	-	0.72	0.066
all bees	farmland	simi	flowers	-	n.s.	
all bees	farmland	flowers	geogr.dist.	-	n.s.	
all bees	farmland	simi	flowers	geogr.dist.	n.s.	
all bees	farmland	simi	geogr.dist.	flowers	n.s.	
all bees	forest edge	simi	geogr.dist.	-	-0.1152	0.629
all bees	forest edge	simi	flowers	-	n.s.	
all bees	forest edge	flowers	geogr.dist.	-	n.s.	
all bees	forest edge	simi	flowers	geogr.dist.	n.s.	
all bees	forest edge	simi	geogr.dist.	flowers	n.s.	
all bees	forest	simi	geogr.dist.	-	0.55	0.025
all bees	forest	simi	flowers	-	n.s.	
all bees	forest	flowers	geogr.dist.	-	n.s.	
all bees	forest	simi	flowers	geogr.dist.	n.s.	
all bees	forest	simi	geogr.dist.	flowers	0.575	0.043
solitary bees	farmland	simi	geogr.dist.	-	n.s.	
solitary bees	farmland	simi	flowers	-	n.s.	
solitary bees	farmland	flowers	geogr.dist.	-	n.s.	
solitary bees	farmland	simi	flowers	geogr.dist.	n.s.	
solitary bees	farmland	simi	geogr.dist.	flowers	n.s.	
solitary bees	forest edge	simi	geogr.dist.	-	n.s.	
solitary bees	forest edge	simi	flowers	-	n.s.	
solitary bees	forest edge	flowers	geogr.dist.	-	n.s.	
solitary bees	forest edge	simi	flowers	geogr.dist.	n.s.	
solitary bees	forest edge	simi	geogr.dist.	flowers	n.s.	
solitary bees	forest	simi	geogr.dist.	-	0.5784	0.01
solitary bees	forest	simi	flowers	-	n.s.	
solitary bees	forest	flowers	geogr.dist.	-	n.s.	
solitary bees	forest	simi	flowers	geogr.dist.	0.5824	0.072
solitary bees	forest	simi	geogr.dist.	flowers	0.683	0.008
Apis mellifera	farmland	abundance	geogr.dist.	-	0.793	0.008
Apis mellifera	farmland	abundance	flowers	-	n.s.	
Apis mellifera	farmland	flowers	geogr.dist.	-	n.s.	
Apis mellifera	farmland	abundance	flowers	geogr.dist.	n.s.	
Apis mellifera	farmland	abundance	geogr.dist.	flowers	0.7966	0.008
Apis mellifera	forest edge	abundance	geogr.dist.	-	n.s.	
Apis mellifera	forest edge	abundance	flowers	-	n.s.	
Apis mellifera	forest edge	flowers	geogr.dist.	-	n.s.	
Apis mellifera	forest edge	abundance	flowers	geogr.dist.	n.s.	
Apis mellifera	forest edge	abundance	geogr.dist.	flowers	n.s.	
Apis mellifera	forest	abundance	geogr.dist.	-	n.s.	
Apis mellifera	forest	abundance	flowers	-	n.s.	
Apis mellifera	forest	flowers	geogr.dist.	-	n.s.	
Apis mellifera	forest	abundance	flowers	geogr.dist.	n.s.	
Apis mellifera	forest	abundance	geogr.dist.	flowers	n.s.	

5.5 Discussion

Justicia flava, the focal plant in this study features a highly generalized pollination system with the very abundant honey bee *Apis mellifera* being the most efficient pollinator (HAGEN 2003, chapter 4 in this thesis), and a high number of additional flower-visiting and pollinating insect species. The plant occurs in a variety of habitats, in dense groups of plants with many flowers ("big bang") in the open areas, and as a typical component of the understory community scattered ("steady state") in the forest interior. The composition of flower visitors differed highly not only between these habitats but also between study sites of the same habitat type. Based on differences in solar radiation (which is higher in open areas compared to the forest interior) and number of flowers, which was also significantly higher outside the forest, other living conditions for flower visiting bees were suspected to be significantly different between habitats as well. Thus, it was not surprising that the composition of flower visitors of *Justicia flava* differed highly between habitats.

The flower visitor composition in the farmland and at the forest edge closely resembled each other (Morisita Horn Similarity: S = 0.99) only due to the high dominance of the honeybee. After focusing on the solitary bee species only, differences in flower visitor composition between the study sites within as well as between habitats became obvious and significant. Visitor composition differed especially between the farmland compared to the other habitats (similarity with forest edge: from 99% to 70%; with forest interior: from 25% to 2%). The similarity between forest edge and forest interior was completely based on the composition of solitary bees, as exclusion of honeybees from analysis did not bring any changes. Only seven out of the 66 insect species visiting the flowers of *J. flava* were found in all three habitat types. These species seemed to be generalists, without specific habitat requirements. Highest correlation in species composition was found between forest edge and forest interior (nine co-occurring species), while only three species were found in the farmland as well as inside the forest. Expectedly, I found a typical edge effect, with the flower visitor composition of the forest edge showing higher similarities with the compositions of the other two habitat types compared to the very low correlation between the flower visitors of farmland and forest interior.

Spatial patterns and correlations differed highly between habitats. Based on Mantel test results, there was no influence of geographical distance on the flower visitor communities and their predictability across habitats at the forest edge but a spatial autocorrelation was conspicuous in farmland and forest interior. However, the pattern of the results differed between the two habitat types. The positive spatial autocorrelation in the composition of flower visitors in the farmland (r = 0.72, p = 0.066) seemed to be primarily due to high spatial autocorrelation in the abundances of honeybees (r = 0.793, p = 0.008), while the influence on solitary bees was smaller and only marginally significant (r = 0.448, p = 0.085). SCHNEIDER & MCNALLY (1993) found that under most conditions colonies of honeybees met their food needs by exploiting relatively small regions of the environment (majority within 1 km of the nest), if enough food is available. *J. flava* and several other plant species showed big flower displays in the farmland. Since *Apis mellifera* and other eusocial bees can communicate the foraging site to nest members and recruit them (ROUBIK 1989), they were presumably attracted by the high amounts of *J. flava* flowers in the farmland, where they could harvest vast quantities of floral rewards to provision their nests. Thus, spatial autocorrelation, found in the farmland, seemed to be a result of the honeybees' behaviour. However, in our analysis, neither flower visitor composition nor abundance of honeybees seemed to be influenced by the number of flowers of *J. flava* or the whole plant community in the study sites. Thus, the food availability was not the limiting factor in the farmland.

In turn, the flowers of *J. flava* and other plant species were found sparsely distributed in the forest understorey (GIKUNGU 2006). Thus, mass-recruiting eusocial bees, which furthermore prefer sunny habitats (MICHENER 2000), play a minor role in flower visitor composition of the forest floor, compared to long-tongued, traplining solitary bees which have a strong preference for flying at ground level and in shaded habitats (KATO ET AL. 2005). The plants usually incorporated in such traplines are "steady state" bloomers (GENTRY 1974) which produce few flowers each day and flower over a long period (JANZEN 1971) and are thus a predictable food source. The food resources might have influenced the flower visitor behaviour to a "spatial-use strategy" or trap-lining strategy (OHASHI ET AL. 2007) rather than a random visitation pattern, in contrast to the study sites outside the forest.

Inside the forest, the effect of geographical distances was found for the flower abundance of *J. flava* as well as for the whole flower visitor communities and even stronger for the community of solitary bees visiting the flowers of *J. flava*. Inside the forest, food resources were the limiting factor for the occurrence and behaviour of the bees.

Real landscapes, of course, are heterogeneous. Their quality as habitat varies across space, and suitable habitat is commonly interspersed in a matrix of unsuitable habitat, which reduces the probability of successful dispersal (e.g. HIRZEL ET AL. 2007). In case of flower visiting bees the suitable habitat is built by the flowers, and the matrix of unsuitable habitat is the non-flowering rest of, in this case, the forest. To exploit the suitable, but widely and scattered distributed food sources, specific foraging methods are needed. Some pollinator species are known to exploit food sources in a traplining manner, including honeybees, bumblebees, euglossine bees, sunbirds and *Heliconius*-butterflies (e.g. RIBBANDS 1949, COMBA 1999, MAKINO & SAKAI 2004, WILLIAMS & THOMSON 1998, GILBERT 1980). Foraging strategies of individuals of single bee species can differ, depending on the number of flowers available to flower visitors. For example, THOMSON & CHITTKA (2001) highlighted that bumblebees showed clear trap-lining behaviour on scattered plants of *Aralia hispida* in central New Brunswick (THOMSON ET AL. 1982); in dense stands of *Solidago* spp. nearby, however, bees of the same species showed no discernable tendency to repeat their flight paths, although they were using small foraging areas. Apparently, the skill with which bees solve a particular foraging task depends substantially on their earlier experience with related tasks (ZHANG & SRINIVASAN 1994). Thus, the behaviour of insects visiting the flowers of *J. flava* seemed to be variable based on the number of flowers available. In the Kakamega farmland, many flowers of several plant species were suspected to offer big amounts of nectar and pollen to their flower visitors, which could be the reason why solitary bees showed a more or less random visitation pattern. In contrast, the small amounts of flowers and the dominance of *J. flava* flowers inside the forest might have led to a trap-lining behaviour. The data suggest that the observed bees in the different habitat types followed different flower visitation strategies due to the availability of food. This might be the reason for the significant spatial autocorrelation inside the forest. Due to the small flower numbers, bees might need to be more “organized” to find enough food. Further studies concerning the flower visitation behaviour of single specimens of bees are urgently needed, due to the fact, that up to now only indirect measures were applied to the behaviour of bees.

Furthermore, studies on bee diversity (see chapter 3) showed that inside the forest significantly more large-sized bee species occurred compared to the other habitat types as the metabolism of larger bees is better adapted to scattered food sources (GATHMANN ET AL. 1994, GATHMANN & TSCHARNTKE 2002) compared to small-sized bees. Habitat does influence the composition of bees, and even within homogeneous habitats (e.g. Kakamega Forest), differences occur. These patterns can also influence the coevolutionary processes. Due to the fact, that bigger bees showed a higher pollination efficiency, the plants inside the forest did not have lower reproductive success compared to the plants in the open areas, where higher flower visitation rates were found. Furthermore, there might be the chance of higher outcrossing rates inside the forest, due to the bees’ foraging behaviour.

The evolution of species interactions can only be fully understood by considering their variation in space and time (THOMPSON & PELLMYR 1992, GOMEZ & ZAMORA 2000), as species interactions commonly coevolve as complex geographic mosaics of populations shaped by differences in local selection and gene flow (HORVITZ & SCHEMSKE 1990, GOMULKIEWICZ ET AL. 2000). But spatial variation must be stable through time to result in local evolutionary specialization of mutualisms, provided the genetically effective population size of the plants is small relative to the area occupied by a particular animal taxon. Because of temporal variation found in the pollinator system of *J. flava* (chapter 3), the effect of spatial variation will be diffused by this temporal variation, which favours a whole assemblage of mutualists rather than one specialized pollinator. The results of the present study support the hypothesis that diffuse selection by a variable assemblage is common in plant-animal mutualisms, especially in the tropics. At least inside the forest, flower visitor composition varied highly on a spatial scale, as shown by low Morisita-Horn values and spatial autocorrelation. Plant species relying on animal vectors for pollination and seed dispersal suffer from a reduction in reproductive success at low abundances, because small patch sizes and increased isolation limit pollen transfer and prevent seed dispersal (AGREN 1996, KUNIN & IWASA 1996, GROOM 1998), and can lead in extreme cases to a reduction in the per capita growth rate, the Allee effect (ALLEE 1931, AMARASEKARE 2004). Interacting species coevolve in different ways in different populations, often creating a geographic mosaic of traits and counter traits. The geographic mosaic theory of coevolution indicates that geographic differences in interactions are an inherent part of the coevolutionary process, driven by variation between habitats as well as variation in habitats. The theory predicts that geographically structure species will tend to coevolve toward a complex spatial mosaic of coevolutionary hotspots and coldspots. Flower visitor communities of *J. flava* were found to differ highly between nearby habitats in composition and reaction to environmental parameters – building a complex spatial mosaic of mutualistic interaction.

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6. GENERAL CONCLUSIONS

In this PhD-thesis, I investigated plant – flower visitor interactions in Kakamega Forest and the surrounding highly structured agricultural area. Due to high anthropogenic pressure the whole landscape mosaic is changing, resulting in a simplification of landscape pattern, which endangers the biodiversity of the area. Especially for bees, which use a high number of different habitats in close vicinity during their life cycle, the presence, configuration and connectivity of the different habitat types is essential and thus of great concern for conservationists.

The thesis is divided in three major topics. First of all, with a food-web approach, the composition, dependency and interaction between the members of the plant – flower visitor networks were investigated. Furthermore, I focused on spatial and temporal changes in the composition of the networks in as well as between the different habitats. As such overall surveys give a broad generalized picture only, I analysed the plant – flower visitor interactions of *Justicia flava* (Acanthaceae) in more detail. I focused not only on the plant and its pollinators but also on their spatial pattern in terms of distribution, spatial autocorrelation, and furthermore the connectance between plant populations through their mobile animal vectors.

6.1 Flower visitor networks

Plant-animal mutualistic networks are interaction webs consisting of two sets of entities, plant and animal species, whose evolutionary dynamics are deeply influenced by the outcomes of the interactions, yielding a diverse array of coevolutionary processes. This coevolutionary change is basically a diffuse process involving sets of species, and pairwise coevolution (JANZEN 1980) is rare in most plant-animal mutualisms (e.g. JORDANO 1987). Networks involving plants and their pollinators or frugivores have recently been shown to exhibit a complex structural characteristic called nestedness, which particularly implies great levels of asymmetric specialization with the core set of generalist species interacting with one another and the most specialised species interacting with the most generalist species only (BASCOMPTE ET AL. 2003, 2006, JORDANO ET AL. 2003). In Kakamega area the flower visitor webs in all three habitat types were highly asymmetric, with the three most involved plant species building 54% – 84% of the network. Interestingly, the most important plants and bees, all of them generalists in terms of pollination partners, were the same in the different habitats whereas the more specialised species differed highly between the habitats, showing habitat dependency. *Apis mellifera* was the most abundant bee species in all habitats, and was involved in 60% - 80% of the interactions in the networks. This is a typical pattern in tropical ecosystems, where the possibility of year-through activity patterns support the eusocial bees in being very successful and dominant (ROUBIK 1979, MICHENER 2000). The genus *Apis* in southern Asia and in Africa and the other highly social bees, the Meliponini, are often the most abundant bees in the tropics. Each such species must be, from the standpoint of floral resources, the ecological equivalent of a number of species of non-social bees as the workers of eusocial species are not only highly abundant but also active all year through. Competition for food by these aggressive generalists has an important influence on the tropical bee faunas (MICHENER 2000). Apart from the negative impacts of humidity on the survival of solitary bees (MICHENER 2000), this is one explanation for the relative scarcity (relative to what would be expected from experience) of bee species in the tropics.

In nested networks, the disappearance of such a strongly interactive species, like *A. mellifera* can lead to profound changes in ecosystem composition, structure, and diversity (SOULÉ AND TERBORGH 1999, TERBORGH ET AL. 1999, OKSANEN & OKSANEN 2000, SCHMITZ ET AL. 2000, SOULÉ ET AL. 2003, SOULÉ ET AL. 2005). However, the extinction of such successful species seems to be rather improbable, although in some parts of the world extreme declines in honeybee-colonies are found. But, depending on the size of a network, the importance of single interaction partners differs. The bigger a pollinator web, and the smaller the relative number of interaction partners per individual is, the less important is the single bee or plant for the persistence of the network. Thus, bigger networks might be less vulnerable to shifts or extinctions in interaction partners (OLESEN & JORDANO 2002). In Kakamega Forest area, I found the bigger networks in the open areas, whereas the network inside the forest was rather small, showing high seasonal fluctuations. Generally, bee species are more adapted to open areas rather than to forests and, in this study, profited highly from the big food/flower supplies, the heterogeneous and thus suitable landscapes as well as the good climatic conditions in the farmland, whereas the small numbers of flowers and the high humidity inside the forest seemed to be more of a challenge to some of the species. However, due to high spatial turnover rates, movements between the habitat types seemed to be probable, and the species- and individual-poor forest profited from the exchange with the species- and individual-rich surrounding open areas. Especially during mass flowering events of forest trees, high numbers of flower visitors must be recruited from the surrounding areas. Thus, every habitat type contributes to the welfare of the plants and animals and a rather high diversity level, and due to movements between habitats, stability of the whole ecosystem might increase. The dimensions of exchange of bees, and thus of genetic material of the plants, between the different habitats, is not known, and future investigations will help to fill the existing gaps of knowledge.

6.2 Justicia flava*: diversity, abundance and spatial patterns of the flower visitors*

Destruction and fragmentation of landscapes can lead to reduction in species richness and abundance of pollinator guilds and thus to a reduction in the reproductive success of plants relying on pollination by these animals. I focused on the abundant herbal self-incompatible plant species *Justicia flava* (Acanthaceae). Comparative results showed that the composition of flower visitors did not only differ clearly between different habitat types, but also between study sites, in close vicinity within the same habitat. Spatial distance had a high significant effect on the composition of flower visitors especially inside the forest, where small numbers of flowers and their scattered distribution challenged the bees during their foraging bouts. As *J. flava* was one of the few plants species flowering throughout the year, it acted as keystone food source for the flower visitors. Thus, bee species composition relied on the distribution of these flowers, and flower visitor behaviour inside the forest seemed to result in traplining behaviour, explaining the spatial autocorrelative pattern which was not found in the composition of solitary bees outside the forest. Interestingly, highest diversity of flower visitors occurred inside the forest, while the flower visitor composition outside the forest was highly dominated by the honeybee, *Apis mellifera*. Up to a distance of 1500m from the forest, the number of bee species visiting the flowers of *J. flava* decreased significantly with increasing distance from the forest whereas the flower visitor composition on study sites farther from the forest did not show any dependency on the distance. This pattern resulted from the different spatial distribution of flowering plant species, with high numbers of flowers of different plant species in the farmland, and few flowers of some keystone species like *J. flava* inside the forest.

Furthermore, I investigated the influence of diversity and abundance of flower visiting insects on the reproductive success of *J. flava*. The reproductive success of the self-incompatible plant was neither influenced by the diversity nor by the abundance of flower visitors, due to the fact, that *J. flava* experienced high visitation frequencies. Even though the plant was not pollinator limited, a diverse and abundant pollinator community is a necessary prerequisite for the survival of this self-incompatible plant, especially in a spatial and seasonal dynamic environment. Investigations on the influence of flower visitors as well as spatial parameters need to be extended to other plant species and their visitors. Especially more specialised pollination systems, like of the oil-providing plant *Momordica foetida* (Cucurbitaceae), which is visited by generalistic as well as specialised bee species (oil-collecting bees of the genus *Ctenoplectra*) need to be investigated in detail in the future.

6.3 Bee diversity pattern depends on focus

A recurring phenomenon in ecological sciences: The level of focus influences the pattern found in the analysis. While focusing on the whole plant-flower visitor network, highest diversity of bees was found in the open, flower rich areas, especially at the forest edge, while only small numbers of bees with high seasonal fluctuations were found inside the forest. Investigations in the diversity of flower visitors of one single plant species (*Justicia flava*) in a specific season showed smallest bee species numbers at the forest edge, with species diversity being highest inside the forest. Especially the high species diversity inside the forest was caused by a high dominance of *Justicia flava* as one of the keystone floral resources, concentrating the bee visitation on a few plant species. Such differences in diversity pattern clarify the high importance of the focus (whole year versus specific season, whole pollinator web versus visitors of a single plant species) in analyses, and the responsibility of the scientists and conservation ecologists, to collect and analyze data carefully, having in mind the potential of different datasets. Depending on the focus, conclusions can be misleading!

6.4 Conservation strategies: conserve the whole landscape mosaic

National parks are important structures to conserve wildlife (especially big vertebrates) in many parts of the world and in the past, conservation in tropical regions was concentrated only in such protected areas (PERFECTO & VANDERMEER 2002). But they become more and more isolated islands within highly developed landscapes (GARDNER ET AL. 2007), and an exclusive focus of conservation efforts on the existing strictly protected area network is insufficient for the successful conservation of biodiversity and ecological integrity (WOODWELL 2002, ARMSWORTH ET AL. 2007, GARDNER ET AL. 2007) especially for organisms like bees. We have seen: for organisms like bees a structured agricultural landscape rather than the conserved National Park is the important structure, and thus needs to get attention. Conservation biologists are increasingly aware that the matrix, within which forest fragments exist, may be as important for conservation as the forest fragments themselves (LAURANCE 1991, THIOLLAY 1995, VANDERMEER & PERFECTO 1997) and that it becomes imperative to understand the conservation value of an entire protected-area network for a wide range of taxonomic groups. There still exist many biodiversity-rich agroecosystems (VANDERMEER & PERFECTO 1997), especially in tropical areas, like the smallholder agricultural areas in the Kakamega Farmland. Attention to such agroecosystems that make up the majority of the matrix may be the key to conservation at the landscape level (VANDERMEER & PERFECTO 1997, PERFECTO & VANDERMEER 2002, FISCHER ET AL. 2006, VANDERMEER & PERFECTO 2007), as patterns of beta diversity and habitat heterogeneity occur at regional, not reserve-size scale (GERING ET AL. 2003). A diverse bee composition and thus a successful pollination of native as well as crop plants, relies on a diverse landscape with a variety of useful habitats for nesting as well as feeding requirements. As the availability of food resources (numbers of flowers) was always positively correlated with abundance as well as diversity of the flower visiting bees in this study, a high proportion of flowering plants in the landscape is one of the key requirements for the conservation of the ecosystem service pollination. In this study, the majority of bee species did not show specific habitat preferences, and were found in all different habitats. If these species need the habitats of the whole mosaic rather than only a small portion of these habitats, needs to be investigated in future. However, my results suggest that the forest understorey is not a reservoir for pollinators of crop plants. The forest itself seemed to rather profit from the bee composition of the farmland and possible migration events into the forest. However, I also found some bee species with possible habitat dependency on the forest. The conservation of these specialised species is of great concern for the conservation of a high biodiversity.

This study and other detailed studies of biodiversity in different land-uses show that smallholder agricultural areas have much to contribute to tropical forest biodiversity conservation (DAILY ET AL. 2001, HUGHES ET AL. 2002, LUCK & DAILY 2003), even though they might have only a limited capacity to compensate for forest loss (LAUBE ET AL. 2008). If human dependency on nature (e.g. through ecosystem services like pollination) becomes widely recognized, society will demand greater environmental stewardship (ARMSWORTH ET AL. 2007). Nature conservation is not widely recognized and thus applied in tropical countries, as poverty in the communities is very high, and people fight for their daily needs rather than for nature conservation. Thus, ecologists also need to make marked efforts to embed human beings within their conceptualization of ecosystems (ARMSWORTH ET AL. 2007), e.g. through socio-economic approaches of alternative income generation.

6.5 Outlook

In this thesis, I found several bee species that occurred in all three habitat types, indicating their tolerance to as well as their dependency on different habitats in their lifecycle, with a highly structured landscape and sufficient food resources as limiting factors. As there is good knowledge about the composition of the flower visiting bees, nothing is known about their nesting and detailed foraging behaviour in East Africa. For a profound conservation of bees and their interacting mutualists, such knowledge is essential and highly needed. Furthermore, we only have the snapshot of spatial distribution with a lot of bee species occurring in the different habitat types rather than a general survey of the dynamics in the bee communities over larger temporal scales. If bee individuals migrate between habitats or if a distinct population of the species exist in each habitat, is not yet clear and needs further investigations. The direct evidence of this pattern is one of the big challenges in pollination ecology, as direct movements of bees are hard to follow and detect. Different methods, like capture-recapture, or radio-tracking need to be improved, to answer this urgent question, which is a necessary basis for the understanding of spatial patterns of pollination interactions as well as for their conservation.

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7. INDEX OF FIGURES

8. INDEX OF TABLES

9. APPENDICES

Appendix 3.1: Number of plant and bee species and abundance of flowers and bees in the different seasons and study sites

Habitat Type	Site	Season	no.of plant species	no. of flowering plant species	mean no. of flowers	no. of plants in interactions	no. of bee species	no. of flower visits	no. of recorded interactions (I)	no. of solitary species	no. of flower visits by solitary bees	no. of social bee species	no. of flower visits by social bees
farmland	Buyangu B	long rain	50	15	105	8	12	93	17	10	12	2	81
	Buyangu B	cold dry	50	15	68	3	3	32	5	2	2	1	30
	Buyangu B	short rain	50	21	633	5	5	13	6	4	6	1	7
	Buyangu B	dry	50	13	41	3	10	26	11	9	20	1	6
	Buyangu B	all seasons	50	29	212	12	19	164	31	17	40	2	124
farmland	Buyangu C	long rain	23	9	32	7	5	215	11	3	5	2	210
	Buyangu C	cold dry	23	11	45	5	11	112	16	8	31	3	81
	Buyangu C	short rain	23	17	159	8	12	78	20	10	26	2	52
	Buyangu C	dry	23	17	55	5	13	68	16	11	24	2	44
	Buyangu C	all seasons	23	20	73	11	25	473	45	22	86	3	387
farmland	Buyangu D	long rain	34	18	94	13	23	145	34	20	42	3	103
	Buyangu D	cold dry	34	8	60	5	17	60	18	15	28	2	32
	Buyangu D	short rain	34	20	199	5	16	69	21	14	20	2	49
	Buyangu D	dry	34	15	61	5	9	38	12	8	8	1	30
	Buyangu D	all seasons	34	23	103	16	44	312	68	41	98	3	214
farmland	Kabrasi B	long rain	26	13	88	4	3	132	6	2	3	1	129
	Kabrasi B	cold dry	26	15	51	3	6	266	7	5	6	1	260
	Kabrasi B	short rain	26	17	89	5	3	32	6	2	7	1	25
	Kabrasi B	dry	26	12	53	3	5	21	6	4	6	1	15
	Kabrasi B	all seasons	26	18	70	9	10	451	17	9	22	1	429
farmland	Kabrasi D	long rain	32	9	67	6	5	21	7	4	4	1	17
	Kabrasi D	cold dry	32	12	33	4	9	41	10	7	11	2	30
	Kabrasi D	short rain	32	19	69	7	8	60	12	6	9	2	51
	Kabrasi D	dry	32	14	45	5	10	26	12	9	10	1	16
	Kabrasi D	all seasons	32	23	54	14	22	148	33	19	34	3	114
farmland	Kabrasi E	long rain	32	17	87	7	10	112	18	8	21	2	91
	Kabrasi E	cold dry	32	13	51	6	14	138	17	12	24	2	114
	Kabrasi E	short rain	32	15	53	3	3	71	5	2	12	1	59
	Kabrasi E	dry	32	12	37	5	4	28	6	3	3	1	25
	Kabrasi E	all seasons	32	25	57	12	22	349	35	19	60	3	289
forest edge	Bukhaywa B	long rain	68	17	94	7	15	25	17	13	14	2	11
	Bukhaywa B	cold dry	68	24	156	6	14	61	17	12	20	2	41
	Bukhaywa B	short rain	68	28	242	5	12	59	13	10	18	2	41
	Bukhaywa B	dry	68	12	61	5	17	57	20	16	32	1	25
	Bukhaywa B	all seasons	68	37	138	10	39	202	53	36	84	3	118
forest edge	Buyangu A	long rain	38	15	111	13	24	197	36	23	85	3	112
	Buyangu A	cold dry	38	21	74	7	9	56	12	9	17	1	39
	Buyangu A	short rain	38	22	269	9	15	59	23	14	32	1	27
	Buyangu A	dry	38	19	70	2	7	26	8	5	6	2	20
	Buyangu A	all seasons	38	30	131	16	42	338	67	38	140	4	198
forest edge	Buyangu E	long rain	27	7	60	5	10	30	13	9	14	1	16
	Buyangu E	cold dry	27	14	55	6	9	40	10	7	11	2	29
	Buyangu E	short rain	27	9	63	7	11	34	17	10	17	1	17

	Buyangu E	dry	27	13	58	5	11	23	12	11	23	0	0
	Buyangu E	all seasons	27	18	59	13	28	127	34	27	65	2	62
forest edge	Buyangu F	long rain	32	8	14	3	4	13	5	3	3	1	10
	Buyangu F	cold dry	32	17	67	8	17	123	24	15	31	2	92
	Buyangu F	short rain	32	16	251	6	10	144	15	9	11	1	133
	Buyangu F	dry	32	13	61	4	14	23	14	12	17	2	6
	Buyangu F	all seasons	32	22	98	12	36	303	46	33	62	3	241
forest edge	Lusero B	long rain	52	18	106	3	12	36	12	11	16	1	20
	Lusero B	cold dry	52	20	124	9	22	72	30	21	48	1	24
	Lusero B	short rain	52	22	330	4	7	29	10	6	10	1	19
	Lusero B	dry	52	20	61	5	20	71	23	19	43	1	28
	Lusero B	all seasons	52	31	155	12	37	208	53	36	117	1	91
forest edge	Upper Camp	long rain	25	7	27	0	0	0	0	0	0	0	0
	Upper Camp	cold dry	25	10	24	3	4	58	3	3	5	1	53
	Upper Camp	short rain	25	9	18	3	2	120	3	1	20	1	100
	Upper Camp	dry	25	8	59	2	12	31	14	11	20	1	11
	Upper Camp	all seasons	25	14	32	5	14	209	18	13	45	1	164
forest	Buyangu G	long rain	60	9	33	1	2	2	1	2	2	0	0
	Buyangu G	cold dry	60	12	56	4	4	273	4	3	3	1	270
	Buyangu G	short rain	60	14	40	4	4	18	4	3	4	1	14
	Buyangu G	dry	60	4	27	2	2	5	3	2	5	0	0
	Buyangu G	all seasons	60	34	39	8	9	298	10	8	14	1	284
forest	Buyangu Hill	long rain	55	7	11	1	2	7	1	1	1	1	6
	Buyangu Hill	cold dry	55	10	35	5	12	23	15	11	11	1	12
	Buyangu Hill	short rain	55	9	40	4	10	23	11	8	13	2	10
	Buyangu Hill	dry	55	5	28	1	6	7	6	5	5	1	2
	Buyangu Hill	all seasons	55	17	28	5	23	60	24	21	30	2	30
forest	Campsite A	long rain	41	8	29	1	2	4	2	1	2	1	2
	Campsite A	cold dry	41	9	32	3	6	100	7	5	5	1	95
	Campsite A	short rain	41	6	22	2	5	17	5	3	3	2	14
	Campsite A	dry	41	4	41	2	7	15	7	6	11	1	4
	Campsite A	all seasons	41	14	31	3	13	136	14	11	21	2	115
forest	Mapera	long rain	47	7	20	1	4	5	2	3	3	1	2
	Mapera	cold dry	47	13	38	2	7	23	8	6	7	1	16
	Mapera	short rain	47	12	58	3	6	12	5	5	5	1	7
	Mapera	dry	47	6	28	1	8	21	9	7	8	1	13
	Mapera	all seasons	47	19	36	5	18	61	18	17	23	1	38
forest	Salazar A	long rain	58	12	45	1	5	7	5	4	4	1	3
	Salazar A	cold dry	58	13	53	1	12	28	10	11	14	1	14
	Salazar A	short rain	58	18	63	1	8	33	10	5	9	3	24
	Salazar A	dry	58	8	72	6	5	18	5	4	5	1	13
	Salazar A	all seasons	58	22	58	6	20	86	24	17	32	3	54
forest	Salazar B	long rain	54	11	15	0	0	0	0	0	0	0	0
	Salazar B	cold dry	54	8	21	2	3	5	3	3	5	0	0
	Salazar B	short rain	54	13	41	3	4	54	4	3	4	1	50
	Salazar B	dry	54	6	13	0	0	0	0	0	0	0	0
	Salazar B	all seasons	54	18	23	3	7	59	7	6	9	1	50

Appendix 3.2:

Bee species and their interaction partners in the farmland; reflecting the order of the pollination network analysis (Figure 3)

bee-species	plant species	Number recorded interactions
Apis mellifera (Apidae)	*Justicia flava* (Acanthaceae)	61
	Bidens pilosa (Asteraceae)	35
	Crassocephalum vitellinum (Asteraceae)	2
	Galinsoga parviflora (Asteraceae)	18
	Commelina diffusa (Asteraceae)	1
	Aspilia plurisetta (Asteraceae)	5
	Aspilia mossambicensis (Asteraceae)	5
	Ageratum conyzoides (Asteraceae)	7
	Solanum mauritianum (Solanaceae)	2
	Tithonia diversifolia (Asteraceae)	11
	Asystasia mysorensis (Acanthaceae)	1
	Leucas deflexa (Lamiaceae)	4
	Asystasia gangetica (Acanthaceae)	3
	Ipomoea wightii (Convolvulaceae)	1
	Phaseolus vulgaris (Fabaceae)	2
	Oxalis latifolia (Oxalidaceae)	9
	Vernonia sp. 1 (Asteraceae)	5
	Acmella calirhiza (Asteraceae)	1
	Manihot esculenta (Euphorbiaceae)	1
	Richardia brasiliensis (Rubiaceae)	1
	Tagetes minuta (Asteraceae)	1
	Justicia striata (Acanthaceae)	1
	Leonotis nepetifolia (Lamiaceae)	3
	Lantana camara (Verbenaceae)	7
	Croton macrostachys (Euphorbiaceae)	2
Halictus (*Seladonia* sp. 2) (Halictidae)	*Justicia flava* (Acanthaceae)	3
	Bidens pilosa (Asteraceae)	2
	Crassocephalum vitellinum (Asteraceae)	1
	Aspilia plurisetta (Asteraceae)	1
	Ageratum conyzoides (Asteraceae)	6
	Asystasia gangetica (Acanthaceae)	1
	Crassocephalum crepidoides (Asteraceae)	1
	Cynoglossum coeruleum (Boraginaceae)	1
Ceratina sp. (Apidae)	*Justicia flava* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	5
	Crassocephalum vitellinum (Asteraceae)	6
	Galinsoga parviflora (Asteraceae)	4
	Commelina diffusa (Commelinaceae)	1
	Aspilia plurisetta (Asteraceae)	1
	Ageratum conyzoides (Asteraceae)	2
	Asystasia gangetica (Acanthaceae)	1
Halictidae	*Bidens pilosa* (Asteraceae)	1
	Crassocephalum vitellinum (Asteraceae)	6
	Aspilia mossambicensis (Asteraceae)	1
	Ageratum conyzoides (Asteraceae)	3
	Solanum mauritianum (Solanaceae)	2
	Tithonia diversifolia (Asteraceae)	2
	Momordica foetida (Cucurbitaceae)	1

Halictus sesdomiale (Halictidae)	*Bidens pilosa* (Asteraceae)	6
	Aspilia plurisetta (Asteraceae)	1
	Ageratum conyzoides (Asteraceae)	1
	Solanum mauritianum (Solanaceae)	2
	Asystasia mysorensis (Acanthaceae)	1
	Justicia calyculata (Acanthaceae)	1
Lasioglossum (*Ctenonomia* sp.)	*Justicia flava* (Acanthaceae)	1
	Galinsoga parviflora (Asteraceae)	1
	Commelina diffusa (Commelinaceae)	2
	Ageratum conyzoides (Asteraceae)	2
	Vernonia sp. 1 (Asteraceae)	1
Megachile bituberculata (Megachilidae)	*Justicia flava* (Acanthaceae)	2
	Bidens pilosa (Asteraceae)	2
	Crassocephalum vitellinum (Asteraceae)	2
	Commelina diffusa (Commelinaceae)	1
	Asystasia mysorensis (Acanthaceae)	1
Braunsapis foveata (Apidae)	*Galinsoga parviflora* (Asteraceae)	1
	Aspilia plurisetta (Asteraceae)	1
	Aspilia mossambicensis (Asteraceae)	1
	Ageratum conyzoides (Asteraceae)	1
Meliponula lendliana (Apidae)	*Justicia flava* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	1
	Commelina diffusa (Commelinaceae)	1
	Tithonia diversifolia (Asteraceae)	1
Meliponula bocandei (Apidae)	*Bidens pilosa* (Asteraceae)	9
	Aspilia plurisetta (Asteraceae)	1
	Aspilia mossambicensis (Asteraceae)	2
	Tithonia diversifolia (Asteraceae)	7
Braunsapis leptozonia (Apidae)	*Bidens pilosa* (Asteraceae)	1
	Aspilia plurisetta (Asteraceae)	1
	Aspilia mossambicensis (Asteraceae)	1
Pseudapis aff. *amoenula* (Halictidae)	*Justicia flava* (Acanthaceae)	1
	Asystasia mysorensis (Acanthaceae)	1
	Oxalis latifolia (Oxalidaceae)	1
Ceratina viridis (Apidae)	*Galinsoga parviflora* (Asteraceae)	1
	Leucas deflexa (Lamiaceae)	1
	Crassocephalum crepidoides (Asteraceae)	1
Ceratina (*Pithitis*) *nasalis* (Apidae)	*Justicia flava* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	2
	Galinsoga parviflora (Asteraceae)	1
Halictus (*Seladonia* sp. 1) (Halictidae)	*Justicia flava* (Acanthaceae)	2
	Bidens pilosa (Asteraceae)	2
	Galinsoga parviflora (Asteraceae)	1
Megachile ianthoptera (Megachilidae)	*Justicia flava* (Acanthaceae)	4
	Bidens pilosa (Asteraceae)	1
	Grass species	1
Amegilla aff. *langi* (Apidae)	*Justicia flava* (Acanthaceae)	15
	Commelina diffusa (Commelinaceae)	1
	Tithonia diversifolia (Asteraceae)	1
Ceratina (*Ctenoceratina*) *ericia* (Apidae)	*Galinsoga parviflora* (Asteraceae)	1
	Asystasia mysorensis (Acanthaceae)	1
Ctenoplectra antinorii (Apidae)	*Commelina diffusa* (Commelinaceae)	1
	Tithonia diversifolia (Asteraceae)	1
Heriades sp. (Megachilidae)	*Justicia flava* (Acanthaceae)	1
	Crassocephalum vitellinum (Asteraceae)	1

Patellapis (*Zonalictus* sp.)	*Solanum mauritianum* (Solanaceae)	1
	Leucas deflexa (Lamiaceae)	1
Lasioglossum (*Sellalictus* sp.) (Halictidae)	*Justicia flava* (Acanthaceae)	1
	Crassocephalum vitellinum (Asteraceae)	2
Nomia aff. *Welwitschii* (Halictidae)	*Justicia flava* (Acanthaceae)	2
	Aspilia plurisetta (Asteraceae)	1
Xylocopa nigrita (Apidae)	*Justicia flava* (Acanthaceae)	1
	Acanthus pubescens (Acanthaceae)	1
Lipotriches orientalis (Lipotriches)	*Justicia flava* (Acanthaceae)	3
	Aspilia mossambicensis (Asteraceae)	1
Pseudanthidium (*Microanthidium*) (Megachilidae)	*Asystasia mysorensis* (Acanthaceae)	1
	Leucas deflexa (Lamiaceae)	1
Xylocopa calens (Apidae)	*Justicia flava* (Acanthaceae)	27
	Phaseolus vulgaris (Fabaceae)	1
Amegilla (*Megamegilla* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla sp (Apidae)	*Justicia flava* (Acanthaceae)	1
Braunsapis aff. *angolensis* (Apidae)	*Justicia flava* (Acanthaceae)	1
Braunsapis aff *leptozonia* (Apidae)	*Bidens pilosa* (Asteraceae)	1
Braunsapis langenburgensis (Apidae)	*Bidens pilosa* (Asteraceae)	1
Braunsapis sp. (Apidae)	*Ocimum hadiens* (Lamiaceae)	1
Colletes sp. (Colletidae)	*Tithonia diversifolia* (Asteraceae)	1
Hylaeus sp. 1 (Colletidae)	*Oxalis corniculatum* (Oxalidaceae)	1
Lasioglossum (*Ctenonomia* sp. 2) (Halictidae)	*Bidens pilosa* (Asteraceae)	1
Lasioglossum (*Rubrihalictus* sp. 2) (Halictidae)	*Justicia flava* (Acanthaceae)	1
Lasioglossum sp. (Halictidae)	*Commelina diffusa* (Commelinaceae)	1
Lipotriches aff. *welwitschii* (Halictidae)	*Justicia flava* (Acanthaceae)	1
Megachile basalis (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile rufipes (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile felina (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile sp. (Megachilidae)	*Crotalaria* sp. (Fabaceae)	1
Megachile dariensis (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Nomia theryi (Halictidae)	*Justicia flava* (Acanthaceae)	1
Patellapis sp. (Halictidae)	*Acanthus pubescens* (Acanthaceae)	1
Patellapis sp. 2 (Halictidae)	*Solanum mauritianum* (Solanaceae)	1
Pleibena hildebrandti (Apidae)	*Galinsoga parviflora* (Asteraceae)	1
Pseudanthidium truncatum (Megachilidae)	*Bidens pilosa* (Asteraceae)	1
Pseudapis sp. (Halictidae)	*Solanum mauritianum* (Solanaceae)	1
Systropha sp. (Halictidae)	*Ipomoea wightii* (Convolvulaceae)	1
Xylocopa (*Xylomellisa* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa aff. *albifrons* (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa carinata (Apidae)	*Justicia flava* (Acanthaceae)	1
Ceratina sp. 6 (Apidae)	*Bidens pilosa* (Asteraceae)	1
Megachilidae	*Justicia flava* (Acanthaceae)	2
Thyreus interruptus (Apidae)	*Justicia flava* (Acanthaceae)	2
Thyreus sp. (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa bouyssoui (Apidae)	*Solanum mauritianum* (Solanaceae)	1
Xylocopa inconstans (Apidae)	*Justicia flava* (Acanthaceae)	2
Amegilla acraensis (Apidae)	*Justicia flava* (Acanthaceae)	2
Ceratina sp. 2 (Apidae)	*Justicia flava* (Acanthaceae)	3
Thyreus calceata (Apidae)	*Justicia flava* (Acanthaceae)	3
Thyreus pictus (Apidae)	*Justicia flava* (Acanthaceae)	2
Xylocopa hottentotta (Apidae)	*Justicia flava* (Acanthaceae)	3
Ceratina sp. 2 (Apidae)	*Aspilia mossambicensis* (Asteraceae)	1

Appendix 3.3:

Plant species and their interaction partners in the farmland; reflecting the order of the pollination network analysis (Figure 3)

plant species	bee-species	Number recorded interactions
Justicia flava (Acanthaceae)	*Apis mellifera* (Apidae)	61
	Halictus (*Seladonia* sp. 2) (Halictidae)	3
	Ceratina sp. (Apidae)	1
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Megachile bituberculata (Megachilidae)	2
	Meliponula lendliana (Apidae)	1
	Pseudapis aff. *amoenula* (Halictidae)	1
	Ceratina (*Pithitis*) *nasalis* (Apidae)	1
	Halictus (*Seladonia* sp. 1) (Halictidae)	2
	Megachile ianthoptera (Megachilidae)	4
	Amegilla aff. *langi* (Apidae)	15
	Heriades sp. (Megachilidae)	1
	Lasioglossum (*Sellalictus* sp.) (Halictidae)	1
	Nomia aff. *welwitschii* (Halictidae)	2
	Xylocopa nigrita (Apidae)	1
	Lipotriches orientalis (Halictidae)	3
	Xylocopa calens (Apidae)	27
	Amegilla (*Megamegilla* sp. 1) (Apidae)	1
	Amegilla sp. (Apidae)	1
	Braunsapis aff. *angolensis* (Apidae)	1
	Lasioglossum (*Rubrihalictus* sp. 2) (Halictidae)	1
	Lipotriches aff *welwitschii* (Halictidae)	1
	Megachile basalis (Megachilidae)	1
	Megachile ciactacombusta (Megachilidae)	1
	Megachile felina (Megachilidae)	1
	Megachile rufipes (Megachilidae)	1
	Nomia theryi (Halictidae)	1
	Xylocopa (*Xylomellisa* sp. 1) (Apidae)	1
	Xylocopa aff. *albifrons* (Apidae)	1
	Xylocopa carinata (Apidae)	1
	Megachilidae	2
	Thyreus interruptus (Apidae)	2
	Thyreus sp (Apidae)	1
	Xylocopa inconstans (Apidae)	2
	Amegilla acraensis (Apidae)	2
	Ceratina (*Ceratina*) sp. 2 (Apidae)	3
	Thyreus calceata (Apidae)	3
	Thyreus pictus (Apidae)	2
	Xylocopa hottentotta (Apidae)	3
Bidens pilosa (Asteraceae)	*Apis mellifera* (Apidae)	35
	Halictus (*Seladonia* sp. 2)	2
	Ceratina sp. (Apidae)	5
	Halictidae	1
	Halictus sesdomiale (Halictidae)	6
	Megachile bituberculata (Megachilidae)	2
	Meliponula lendliana (Apidae)	1
	Meliponula bocandei (Apidae)	9
	Braunsapis leptozonia (Apidae)	1
	Ceratina (*Pithitis*) *nasalis* (Apidae)	2

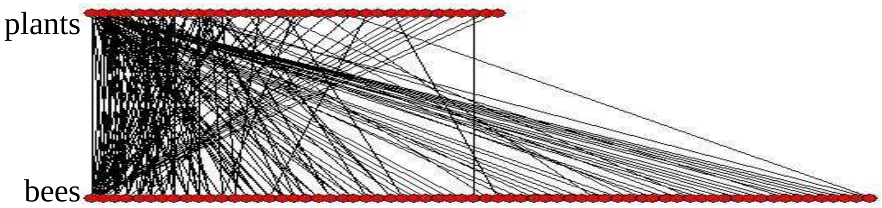
	Halictus (*Seladonia* sp. 1) (Halictidae)	2
	Megachile ianthoptera (Megachilidae)	1
	Braunsapis aff. *leptozonia* (Apidae)	1
	Braunsapis langenburgensis (Apidae)	1
	Lasioglossum (*Ctenonomia* sp. 2)	1
	Pseudanthidium truncatum (Megachilidae)	1
	Ceratina sp. 6 (Apidae)	1
Crassocephalum vitellinum (Asteraceae)	*Apis mellifera* (Apidae)	2
	Halictus (*Seladonia* sp. 2) (Halictidae)	1
	Ceratina sp. (Apidae)	6
	Halictidae	6
	Megachile bituberculata (Megachilidae)	2
	Heriades sp. (Megachilidae)	1
	Lasioglossum (*Sellalictus* sp.) (Halictidae)	2
Galinsoga parviflora (Asteraceae)	*Apis mellifera* (Apidae)	18
	Ceratina sp. (Apidae)	4
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Braunsapis foveata (Apidae)	1
	Ceratina viridis (Apidae)	1
	Ceratina (*Pithitis*) *nasalis* (Apidae)	1
	Halictus (*Seladonia* sp. 1) (Halictidae)	1
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	1
	Pleibena hildebrandtii (Apidae)	1
Commelina diffusa (Commelinaceae)	*Apis mellifera* (Apidae)	1
	Ceratina sp. (Apidae)	1
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	2
	Megachile bituberculata (Megachilidae)	1
	Meliponula lendliana (Apidae)	1
	Amegilla aff. *langi* (Apidae)	1
	Ctenoplectra antinorii (Apidae)	1
	Lasioglossum sp. (Halictidae)	1
Aspilia plurisetta (Asteraceae)	*Apis mellifera* (Apidae)	5
	Halictus (*Seladonia* sp. 2) (Halictidae)	1
	Ceratina sp. (Apidae)	1
	Halictus sesdomiale (Halictidae)	1
	Braunsapis foveata (Apidae)	1
	Meliponula bocandei (Apidae)	1
	Braunsapis leptozonia (Apidae)	1
	Nomia aff. *welwitschii* (Halictidae)	1
Aspilia mossambicensis (Asteraceae)	*Apis mellifera* (Apidae)	5
	Halictidae	1
	Braunsapis foveata (Apidae)	1
	Meliponula bocandei (Apidae)	2
	Braunsapis leptozonia (Apidae)	1
	Lipotriches orientalis (Halictidae)	1
	Ceratina sp. 2 (Apidae)	1
Ageratum conyzoides (Asteraceae)	*Apis mellifera* (Apidae)	7
	Halictus (*Seladonia* sp. 2)	6
	Ceratina sp. (Apidae)	2
	Halictidae	3
	Halictus sesdomiale (Halictidae)	1
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	2
	Braunsapis foveata (Apidae)	1
Solanum mauritianum (Solanaceae)	*Apis mellifera* (Apidae)	2
	Halictidae	2

	Halictus sesdomiale (Halictidae)	2
	Patellapis (*Zonalictus* sp.) (Halictidae)	1
	Patellapis sp. 2 (Halictidae)	1
	Pseudapis sp. (Halictidae)	1
	Xylocopa bouyssoui (Apidae)	1
Tithonia diversifolia (Asteraceae)	*Apis mellifera* (Apidae)	11
	Halictidae	2
	Meliponula lendliana (Apidae)	1
	Meliponula bocandei (Apidae)	7
	Amegilla aff. *langi* (Apidae)	1
	Ctenoplectra antinorii (Apidae)	1
	Colletes sp. (Colletidae)	1
Asystasia mysorensis (Acanthaceae)	*Apis mellifera* (Apidae)	1
	Halictus sesdomiale (Halictidae)	1
	Megachile bituberculata (Megachilidae)	1
	Pseudapis aff. *amoenula* (Halictidae)	1
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	1
	Pseudanthidium (*Microanthidium*) (Megachilidae)	1
Leucas deflexa (Lamiaceae)	*Apis mellifera* (Apidae)	4
	Ceratina viridis (Apidae)	1
	Patellapis (*Zonalictus* sp.) (Halictidae)	1
	Pseudanthidium (*Microanthidium*) (Megachilidae)	1
Asystasia gangetica (Acanthaceae)	*Apis mellifera* (Apidae)	3
	Halictus (*Seladonia* sp. 2) (Halictidae)	1
	Ceratina sp. (Apidae)	1
Acanthus pubescens (Acanthaceae)	*Xylocopa nigrita* (Apidae)	1
	Patellapis sp. (Halictidae)	1
Crassocephalum crepidoides (Asteraceae)	*Halictus* (*Seladonia* sp. 2) (Halictidae)	1
	Ceratina viridis (Apidae)	1
Ipomoea wightii (Convolvulaceae)	*Apis mellifera* (Apidae)	1
	Systropha sp. (Halictidae)	1
Phaseolus vulgaris (Fabaceae)	*Apis mellifera* (Apidae)	2
	Xylocopa calens (Apidae)	1
Oxalis latifolia (Oxalidaceae)	*Apis mellifera* (Apidae)	9
	Pseudapis aff *amoenula* (Halictidae)	1
Vernonia sp. 1 (Asteraceae)	*Apis mellifera* (Apidae)	5
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
Crotalaria sp. (Fabaceae)	*Megachile* sp. (Megachilidae)	1
Cynoglossum coeruleum (Boraginaceae)	*Halictus* (*Seladonia* sp. 2) (Halictidae)	1
Ipomoea purpurea (Convolvulaceae)	*Ceratina* sp. 3 (Apidae)	1
Justicia calyculata (Acanthaceae)	*Halictus sesdomiale* (Halictidae)	1
Grass species	*Megachile ianthoptera* (Megachilidae)	1
Momordica foetida (Ccurbitaceae)	Halictidae	1
Oxalis corniculatum (Oxalidaceae)	*Hylaeus* sp. 1 (Colletidae)	1
Acmella calirhiza (Asteraceae)	*Apis mellifera* (Apidae)	1
Manihot esculenta (Euphorbiaceae)	*Apis mellifera* (Apidae)	1
Richardia brasiliensis (Rubiaceae)	*Apis mellifera* (Apidae)	1
Tagetes minuta (Asteraceae)	*Apis mellifera* (Apidae)	1
Justicia striata (Acanthaceae)	*Apis mellifera* (Apidae)	1
Leonotis nepetifolia (Lamiaceae)	*Apis mellifera* (Apidae)	3
Ocimum hadiens (Lamiaceae)	*Braunsapis* sp. (Apidae)	1
Lantana camara (Verbenaceae)	*Apis mellifera* (Apidae)	7
Croton macrostachys (Euphorbiaceae)	*Apis mellifera* (Apidae)	2

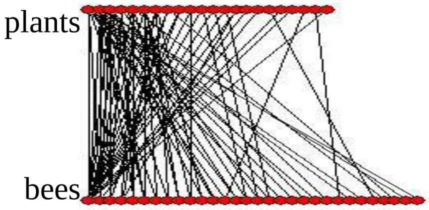
Appendix 3.4:

Farmland: A network approach to plant-bee mutualisms in the different seasons. Every red dot indicates a bee or plant species. A bee and a plant interact, if there is a qualitative link (black line) between them; bees and plants are ordered after the number of interaction partners and the number of interactions with their partners. Thus, generalist interaction partners are found on the left, specialists on the right.

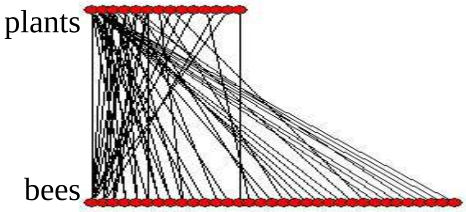
Farmland



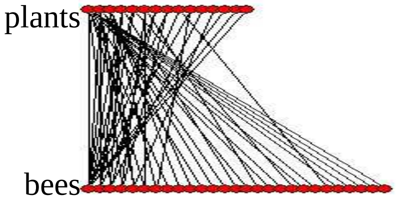
Longrain Season



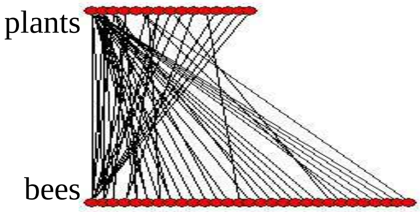
Colddry Season



Shortrain Season



Dry Season



Appendix 3.5:

Bee species and their interaction partners at the forest edge; reflecting the order of the pollination network analysis (Figure 3)

bee-species	plant species	Number recorded interactions
Apis mellifera (Apidae)	*Justicia flava* (Acanthaceae)	61
	Justicia striata (Acanthaceae)	7
	Bidens pilosa (Asteraceae)	8
	Solanum mauritianum (Solanaceae)	1
	Asystasia gangetica (Acanthaceae)	11
	Emilia discifolia (Asteraceae)	1
	Justicia calyculata (Acanthaceae)	4
	Crassocephalum vitellinum (Asteraceae)	5
	Galinsoga parviflora (Asteraceae)	6
	Lantana camara (Verbenaceae)	10
	Ageratum conyzoides (Asteraceae)	3
	Acmella calirhiza (Asteraceae)	2
	Asystasia mysorensis (Acanthaceae)	2
	Desmodium repandum (Fabaceae)	1
	Leucas deflexa (Lamiaceae)	2
	Pavonia urens (Malvaceae)	4
	Cordia abyssinica (Boraginaceae)	2
	Justicia glabra (Acanthaceae)	2
	Psidium guajava (Myrtaceae)	3
	Zea mays (Poaceae)	1
Halictidae	*Justicia flava* (Acanthaceae)	1
	Justicia striata (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	5
	Solanum mauritianum (Solanaceae)	4
	Emilia discifolia (Asteraceae)	2
	Justicia calyculata (Acanthaceae)	1
	Crassocephalum vitellinum (Asteraceae)	2
	Galinsoga parviflora (Asteraceae)	1
	Momordica foetida (Cucurbitaceae)	2
	Ageratum conyzoides (Asteraceae)	1
	Pavonia urens (Malvaceae)	1
	Basella alba (Basellaceae)	1
	Microglossa pyrifolia (Asteraceae)	1
Ceratina sp. (Apidae)	*Justicia flava* (Acanthaceae)	7
	Justicia striata (Acanthaceae)	3
	Bidens pilosa (Asteraceae)	2
	Solanum mauritianum (Solanaceae)	1
	Asystasia gangetica (Acanthaceae)	4
	Emilia discifolia (Asteraceae)	1
	Crassocephalum vitellinum (Asteraceae)	3
	Galinsoga parviflora (Asteraceae)	1
	Momordica foetida (Cucurbitaceae)	2
	Acmella calirhiza (Asteraceae)	1
	Asystasia mysorensis (Acanthaceae)	1
	Solanum nigrum (Solanaceae)	1
Halictus (*Seladonia* sp. 2) (Halictidae)	*Justicia flava* (Acanthaceae)	4

	Emilia discifolia (Asteraceae)	2
	Crassocephalum vitellinum (Asteraceae)	2
	Acanthus pubescens (Acanthaceae)	1
	Ageratum conyzoides (Asteraceae)	3
	Dyschoriste nagchana (Acanthaceae)	1
Lasioglossum (*Ctenonomia* sp.) (Halictidae)	*Justicia striata* (Acanthaceae)	1
	Emilia discifolia (Asteraceae)	1
	Crassocephalum vitellinum (Asteraceae)	1
	Galinsoga parviflora (Asteraceae)	1
	Dyschoriste nagchana (Acanthaceae)	1
	Conyza sp. (Asteraceae)	1
Ceratina (*Ctenoceratina*) *ericia* (Apidae)	*Justicia flava* (Acanthaceae)	2
	Justicia striata (Acanthaceae)	2
	Bidens pilosa (Asteraceae)	1
	Justicia calyculata (Acanthaceae)	1
	Crotalaria sp (Fabaceae)	1
Meliponula lendliana (Apidae)	*Justicia flava* (Acanthaceae)	1
	Justicia striata (Acanthaceae)	1
	Solanum mauritianum (Solanaceae)	4
	Crassocephalum vitellinum (Asteraceae)	1
	Galinsoga parviflora (Asteraceae)	1
Ceratina viridis (Apidae)	*Justicia flava* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	1
	Asystasia gangetica (Acanthaceae)	1
	Galinsoga parviflora (Asteraceae)	1
Halictus (*Seladonia* sp. 1) (Halictidae)	*Bidens pilosa* (Asteraceae)	1
	Emilia discifolia (Asteraceae)	1
	Crassocephalum vitellinum (Asteraceae)	1
	Desmodium sp. (Fabaceae)	1
Megachilidae	*Justicia flava* (Acanthaceae)	8
	Acmella calirhiza (Asteraceae)	1
	Crotalaria sp (Fabaceae)	1
	Desmodium repandum (Fabaceae)	1
Xylocopa carinata (Apidae)	*Justicia flava* (Acanthaceae)	2
	Acanthus pubescens (Acanthaceae)	1
	Caesalpinia decapetala (Caesalpiniaceea)	1
	Clerodendrum myricoides (Verbenaceae)	1
Amegilla aff. *langi* (Apidae)	*Justicia flava* (Acanthaceae)	7
	Lantana camara (Verbenaceae)	1
	Lantana trifolia (Verbenaceae)	1
Braunsapis foveata (Apidae)	*Asystasia gangetica* (Acanthaceae)	1
	Momordica foetida (Cucurbitaceae)	1
	Dyschoriste nagchana (Acanthaceae)	1
Ceratina (*Pithitis*) *nasalis* (Apidae)	*Justicia flava* (Acanthaceae)	2
	Asystasia gangetica (Acanthaceae)	1
	Justicia calyculata (Acanthaceae)	1
Heriades sp. (Megachilidae)	*Justicia striata* (Acanthaceae)	1
	Asystasia gangetica (Acanthaceae)	1
	Hibiscus occidentalis (Malvaceae)	1
Meliponula bocandei (Apidae)	*Bidens pilosa* (Asteraceae)	1
	Caesalpinia decapetala (Caesalpiniaceae)	1
	Zea mays (Poaceae)	1
Xylocopa nigrita (Apidae)	*Justicia flava* (Acanthaceae)	2
	Acanthus pubescens (Acanthaceae)	7
	Caesalpinia decapetala (Caesalpiniaceae)	3

Allodape interrupta (Apidae)	*Justicia striata* (Acanthaceae)	1
	Justicia calyculata (Acanthaceae)	1
Amegilla (*Megamegilla* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	8
	Oxalis corniculatum (Oxalidaceae)	1
Amegilla acraensis (Apidae)	*Justicia flava* (Acanthaceae)	17
	Lantana camara (Verbenaceae)	1
Ceratina (*Ctenoceratina*) near *lineola* (Apidae)	*Justicia flava* (Acanthaceae)	1
	Lantana camara (Verbenaceae)	1
Ctenoplectra terminalis (Apidae)	*Bidens pilosa* (Asteraceae)	1
	Momordica foetida (Cucurbitaceae)	1
Halictus sesdomiale (Halictidae)	*Justicia flava* (Acanthaceae)	2
	Solanum mauritianum (Solanaceae)	2
Lasioglossum (*Sellalictus* sp.) (Halictidae)	*Justicia striata* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	1
Megachile ?*fulvitarsis* (Megachilidae)	*Justicia flava* (Acanthaceae)	2
	Bidens pilosa (Asteraceae)	1
Megachile ciacta combusta (Megachilidae)	*Justicia flava* (Acanthaceae)	1
	Asystasia mysorensis (Acanthaceae)	1
Megachile bituberculata (Megachilidae)	*Justicia flava* (Acanthaceae)	4
	Justicia striata (Acanthaceae)	1
Nomia (*Leuconomia* sp. 1) (Halictidae)	*Justicia flava* (Acanthaceae)	2
	Ageratum conyzoides (Asteraceae)	1
Nomia (*Leuconomia* sp. 2) (Halictidae)	*Justicia flava* (Acanthaceae)	1
	Bidens pilosa (Asteraceae)	1
Nomia (*Leuconomia* sp. 3) (Halictidae)	*Justicia calyculata* (Acanthaceae)	1
	Lantana camara (Verbenaceae)	1
Patellapis (*Zonalictus* sp.) (Halictidae)	*Solanum mauritianum* (Solanaceae)	2
	Hibiscus occidentalis (Malvaceae)	1
Thrinchostoma sp (Halictidae)	*Justicia flava* (Acanthaceae)	1
	Leucas deflexa (Lamiaceae)	1
Thyreus pictus (Apidae)	*Justicia flava* (Acanthaceae)	14
	Justicia calyculata (Acanthaceae)	1
Xylocopa bouyssoui (Apidae)	*Justicia flava* (Acanthaceae)	2
	Acanthus pubescens (Acanthaceae)	1
Xylocopa torrida (Apidae)	*Justicia flava* (Acanthaceae)	1
	Clerodendrum myricoides (Verbenaceae)	1
Aframegilla sp. (Apidae)	*Solanum mauritianum* (Solanaceae)	1
Amegilla bipartita (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla mimadvena (Apidae)	*Justicia flava* (Acanthaceae)	9
Amegilla sp. (Apidae)	*Justicia flava* (Acanthaceae)	4
Braunsapis angolensis (Apidae)	*Asystasia gangetica* (Acanthaceae)	1
Braunsapis lyrata (Apidae)	*Lantana camara* (Verbenaceae)	1
Ceratina (*Ceratina*) sp. 1 (Apidae)	*Justicia flava* (Acanthaceae)	1
Ceratina (*Ceratina*) sp. 2 (Apidae)	*Emilia discifolia* (Acanthaceae)	1
Ceratina (*Ceratina*) sp. 3 (Apidae)	*Asystasia gangetica* (Acanthaceae)	1
Ceratina aff. *moerenhouti* (Apidae)	*Justicia striata* (Acanthaceae)	1
Ceratina sp. 2 (Apidae)	*Asystasia gangetica* (Acanthaceae)	1
	Thunbergia alata (Acanthaceae)	1
Coelioxys sp. 4 (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Colletes sp. (Colletidae)	*Solanum mauritianum* (Solanaceae)	1
Creightoniella ithanoptera (Apidae)	*Justicia flava* (Acanthaceae)	1
Euaspis abdominalis (Megachilidae)	*Justicia flava* (Acanthaceae)	2
Euaspis erythros (Megachilidae)	*Justicia flava* (Acanthaceae)	2
Lasioglossum (*Sellalictus* sp. 2) (Halictidae)	*Momordica foetida* (Cucurbitaceae)	1

Hylaeus sp. 1 (Colletidae)	*Justicia calyculata* (Acanthaceae)	1
Lasioglossum (*Rubrihalictus* sp. 2) (Halictidae)	*Asystasia gangetica* (Acanthaceae)	1
Lasioglossum sp. (Halictidae)	*Justicia striata* (Acanthaceae)	1
Lipotriches aff. *panganina* (Halictidae)	*Justicia flava* (Acanthaceae)	1
Lipotriches aff. *welwitschii* (Halictidae)	*Justicia flava* (Acanthaceae)	1
Lipotriches sp. (Halictidae)	*Solanum mauritianum* (Solanaceae)	1
Megachile aff. *bengualense* (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile ciactacombusta (Megachilidae)	*Justicia flava* (Acanthaceae)	6
Megachile felina (Megachilidae)	*Justicia flava* (Acanthaceae)	8
Megachile ianthoptera (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile nifipennis (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile niveicauda (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile picta (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile torrida (Megachilidae)	*Justicia flava* (Acanthaceae)	2
Megachile rufipes (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Meliponula ferruginea (Megachilidae)	*Zea mays* (Poaceae)	1
Nomia sp. (Halictidae)	*Justicia flava* (Acanthaceae)	1
Nomia viridicincta (Halictidae)	*Justicia striata* (Acanthaceae)	1
Pachyanthidium aff. *bengalense* (Megachilidae)	*Emilia discifolia* (Acanthaceae)	1
Patellapis (*Zonalictus* sp. 7) (Apidae)	*Justicia flava* (Acanthaceae)	1
Patellapis (*Zonalictus* sp.) (Apidae)	*Lantana camara* (Verbenaceae)	1
Patellapis fonalictus (Apidae)	*Solanum mauritianum* (Solanaceae)	1
Pseudapis aff. *amoenula* (Halictidae)	*Justicia flava* (Acanthaceae)	1
Pseudapis sp. (Halictidae)	*Galinsoga parviflora* (Acanthaceae)	1
Systropha sp. (Halictidae)	*Momordica foetida* (Cucurbitaceae)	1
Thyreus bouyssoui (Apidae)	*Justicia flava* (Acanthaceae)	1
Thyreus calceata (Apidae)	*Justicia flava* (Acanthaceae)	3
Thyreus interruptus (Apidae)	*Justicia flava* (Acanthaceae)	5
Thyreus sp. (Apidae)	*Justicia flava* (Acanthaceae)	4
Xylocopa (*Kortosoma* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	3
Xylocopa calens (Apidae)	*Justicia flava* (Acanthaceae)	16
Xylocopa erythrina (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa flavorufa (Apidae)	*Acanthus pubescens* (Acanthaceae)	2
Xylocopa (*Xylomelissa* sp. 2) (Apidae)	*Acanthus pubescens* (Acanthaceae)	1
Xylocopa hottentotta (Apidae)	*Justicia flava* (Acanthaceae)	6
Xylocopa imitator (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa melissa (Apidae)	*Justicia flava* (Acanthaceae)	5

Appendix 3.6:

Plant species and their interaction partners at the forest edge; reflecting the order of the pollination network analysis (Figure 3)

plant species	bee-species	Number recorded interactions
Justicia flava (Acanthaceae)	*Apis mellifera* (Apidae)	61
	Halictidae	1
	Ceratina sp. (Apidae)	7
	Halictus (*Seladonia* sp. 2) (Halictidae)	4
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	2
	Meliponula lendliana (Apidae)	1
	Ceratina viridis (Apidae)	1
	Megachilidae	8
	Xylocopa carinata (Apidae)	2
	Amegilla aff. *langi* (Apidae)	7
	Ceratina (*Pithitis*) *nasalis* (Apidae)	2
	Xylocopa nigrita (Apidae)	2
	Amegilla (*Megamegilla* sp. 1) (Apidae)	8
	Amegilla acraensis (Apidae)	17
	Ceratina (*Ctenoceratina*) near *lineola* (Apidae)	1
	Halictus sesdomiale (Halictidae)	2
	Megachile ? fulvitarsis (Megachilidae)	2
	Megachile rufipes (Megachilidae)	1
	Megachile bituberculata (Megachilidae)	4
	Nomia (*Leuconomia* sp. 1) (Halictidae)	2
	Nomia (*Leuconomia* sp. 2) (Halictidae)	1
	Thrinchostoma sp. (Halictidae)	1
	Thyreus pictus (Apidae)	14
	Xylocopa bouyssoui (Apidae)	2
	Xylocopa torrida (Apidae)	1
	Amegilla bipartita (Apidae)	1
	Amegilla mimadvena (Apidae)	9
	Amegilla sp. (Apidae)	4
	Ceratina sp. 1 (Apidae)	1
	Coelioxys sp. 4 (Megachilidae)	1
	Creightoniella ithanoptera (Apidae)	1
	Euaspis abdominalis (Megachilidae)	2
	Euaspis erythros (Megachilidae)	2
	Lipotriches aff. *panganina* (Halictidae)	1
	Lipotriches aff. *welwitschii* (Halictidae)	1
	Megachile aff. *bengualense* (Megachilidae)	1
	Megachile ciactacombusta (Megachilidae)	6
	Megachile felina (Megachilidae)	8
	Megachile ianthoptera (Megachilidae)	1
	Megachile nifipennis (Megachilidae)	1
	Megachile niveicauda (Megachilidae)	1
	Megachile picta (Megachilidae)	1
	Megachile torrida (Megachilidae)	2
	Megachile bituberculata (Megachilidae)	1
	Nomia sp (Halictidae)	1
	Patellapis (*Zonalictus* sp. 7) (Halictidae)	1
	Pseudapis aff. *amoenula* (Halictidae)	1
	Thyreus bouyssoui (Apidae)	1
	Thyreus calceata (Apidae)	3

	Thyreus interruptus (Apidae)	5
	Thyreus sp. (Apidae)	4
	Xylocopa (*Kortosoma* sp. 1) (Apidae)	3
	Xylocopa calens (Apidae)	16
	Xylocopa erythrina (Apidae)	1
	Xylocopa hottentotta (Apidae)	6
	Xylocopa imitator (Apidae)	1
	Xylocopa melissa (Apidae)	5
Justicia striata (Acanthaceae)	*Apis mellifera* (Apidae)	7
	Halictidae	1
	Ceratina sp. (Apidae)	3
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	2
	Meliponula lendliana (Apidae)	1
	Heriades sp. (Colletidae)	1
	Allodape interrupta (Apidae)	1
	Lasioglossum (*Sellalictus* sp.) (Halictidae)	1
	Megachile bituberculata (Megachilidae)	1
	Ceratina aff. *moerenhouti* (Apidae)	1
	Lasioglossum sp. (Halictidae)	1
	Nomia viridicincta (Halictidae)	1
Bidens pilosa (Asteraceae)	*Apis mellifera* (Apidae)	8
	Halictidae	5
	Ceratina sp. (Apidae)	2
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	1
	Ceratina viridis (Apidae)	1
	Halictus (*Seladonia* sp. 1) (Halictidae)	1
	Meliponula bocandei (Apidae)	1
	Ctenoplectra terminalis (Apidae)	1
	Lasioglossum (*Sellalictus* sp.) (Halictidae)	1
	Megachile ?*fulvitarsis* (Megachilidae)	1
	Nomia (*Leuconomia* sp. 2) (Halictidae)	1
Solanum mauritianum (Solanaceae)	*Apis mellifera* (Apidae)	1
	Halictidae	4
	Ceratina sp. (Apidae)	1
	Meliponula lendliana (Apidae)	4
	Halictus sesdomiale (Halictidae)	2
	Patellapis (*Zonalictus* sp.) (Halictidae)	2
	Aframegilla sp. (Apidae)	1
	Colletes sp. (Colletidae)	1
	Lipotriches sp. (Halictidae)	1
	Patellapis fonalictus (Halictidae)	1
Asystasia gangetica (Acanthaceae)	*Apis mellifera* (Apidae)	11
	Ceratina sp. (Apidae)	4
	Ceratina viridis (Apidae)	1
	Braunsapis foveata (Apidae)	1
	Ceratina (*Pithitis*) *nasalis* (Apidae)	1
	Heriades sp. (Megachilidae)	1
	Braunsapis angolensis (Apidae)	1
	Ceratina sp. 3 (Apidae)	1
	Ceratina sp. 2 (Apidae)	1
	Lasioglossum (*Rubrihalictus* sp. 2) (Halictidae)	1
Emilia discifolia (Asteraceae)	*Apis mellifera* (Apidae)	1
	Halictidae	2
	Ceratina sp. (Apidae)	1

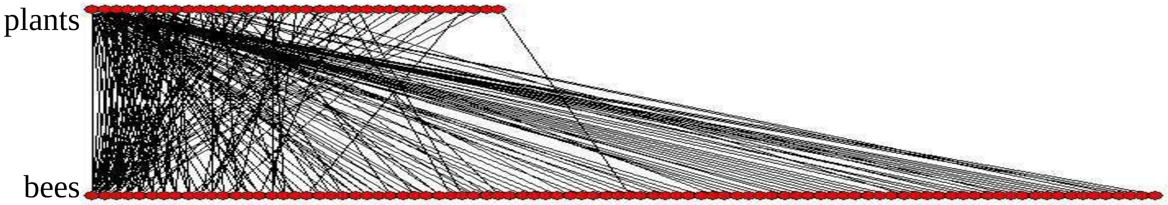
	Halictus (*Seladonia* sp. 2) (Halictidae)	2
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Halictus (*Seladonia* sp. 1) (Halictidae)	1
	Ceratina sp. 2 (Apidae)	1
	Pachyanthidium aff. *bengalense* (Megachilidae)	1
Justicia calyculata (Acanthaceae)	*Apis mellifera* (Apidae)	4
	Halictidae	1
	Ceratina (*Ctenoceratina*) *ericia* (Apidae)	1
	Ceratina (*Pithitis*) *nasalis* (Apidae)	1
	Allodape interrupta (Apidae)	1
	Nomia (*Leuconomia* sp. 3) (Halictidae)	1
	Thyreus pictus (Apidae)	1
	Hylaeus sp. 1 (Colletidae)	1
Crassocephalum vitellinum (Asteraceae)	*Apis mellifera* (Apidae)	5
	Halictidae	2
	Ceratina sp. (Apidae)	3
	Halictus (*Seladonia* sp. 2) (Halictidae)	2
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Meliponula lendliana (Apidae)	1
	Halictus (*Seladonia* sp. 1) (Halictidae)	1
Galinsoga parviflora (Asteraceae)	*Apis mellifera* (Apidae)	6
	Halictidae	1
	Ceratina sp. (Apidae)	1
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Meliponula lendliana (Apidae)	1
	Ceratina viridis (Apidae)	1
	Pseudapis sp. (Halictidae)	1
Lantana camara (Verbenaceae)	*Apis mellifera* (Apidae)	10
	Amegilla aff *langi* (Apidae)	1
	Amegilla acraensis (Apidae)	1
	Ceratina (*Ctenoceratina*) near *lineola* (Apidae)	1
	Nomia (*Leuconomia* sp. 3) (Halictidae)	1
	Braunsapis lyrata (Apidae)	1
	Patellapis (*Zonalictus* sp.) (Halictidae)	1
Acanthus pubescens (Acanthaceae)	*Halictus* (*Seladonia* sp. 2) (Halictidae)	1
	Xylocopa carinata (Apidae)	1
	Xylocopa nigrita (Apidae)	7
	Xylocopa bouyssoui (Apidae)	1
	Xylocopa flavorufa (Apidae)	2
	Xylocopa imitator (Apidae)	1
Momordica foetida (Cucurbitaceae)	Halictidae	2
	Ceratina sp. (Apidae)	2
	Braunsapis foveata (Apidae)	1
	Ctenoplectra terminalis (Apidae)	1
	Lasioglossum (*Ctenonomia* sp. 2) (Halictidae)	1
	Systropha sp. (Halictidae)	1
Ageratum conyzoides (Asteraceae)	*Apis mellifera* (Apidae)	3
	Halictidae	1
	Halictus (*Seladonia* sp. 2) (Halictidae)	3
	Nomia (*Leuconomia* sp. 1) (Halictidae)	1
Acmella calirhiza (Asteraceae)	*Apis mellifera* (Apidae)	2
	Ceratina sp. (Apidae)	1
	Megachilidae	1
Asystasia mysorensis (Acanthaceae)	*Apis mellifera* (Apidae)	2
	Ceratina sp. (Apidae)	1

	Megachile ciactacombusta (Megachilidae)	1
Caesalpinia decapetala (Caesalpiniaceae)	*Xylocopa carinata* (Apidae)	1
	Meliponula bocandei (Apidae)	1
	Xylocopa nigrita (Apidae)	3
Dyschoriste nagchana (Acanthaceae)	*Halictus* (*Seladonia* sp. 2) (Halictidae)	1
	Lasioglossum (*Ctenonomia* sp.) (Halictidae)	1
	Braunsapis foveata (Apidae)	1
Zea mays (Poaceae)	*Apis mellifera* (Apidae)	1
	Meliponula bocandei (Apidae)	1
	Meliponula ferruginea (Apidae)	1
Clerodendrum myricoides (Verbenaceae)	*Xylocopa carinata* (Apidae)	1
	Xylocopa torrida (Apidae)	1
Crotalaria sp. (Fabaceae)	*Ceratina* (*Ctenoceratina*) *ericia* (Apidae)	1
	Megachilidae	1
Desmodium repandum (Fabaceae)	*Apis mellifera* (Apidae)	1
	Megachilidae	1
Hibiscus occidentalis (Malvaceae)	*Heriades* sp. (Megachilidae)	1
	Patellapis (*Zonalictus* sp.) (Halictidae)	1
Leucas deflexa (Lamiaceae)	*Apis mellifera* (Apidae)	2
	Thrinchostoma sp (Halictidae)	1
Pavonia urens (Malvaceae)	*Apis mellifera* (Apidae)	4
	Halictidae	1
Basella alba (Basellaceae)	Halictidae	1
Conyza sp. (Asteraceae)	*Lasioglossum* (*Ctenonomia* sp.) (Halictidae)	1
Cordia abyssinica (Boraginaceae)	*Apis mellifera* (Apidae)	2
Desmodium sp. (Fabaceae)	*Halictus* (*Seladonia* sp. 1) (Halictidae)	1
Justicia glabra (Acanthaceae)	*Apis mellifera* (Apidae)	2
Lantana trifolia (Verbenaceae)	*Amegilla* aff. *langi* (Apidae)	1
Microglossa pyrifolia (Asteraceae)	Halictidae	1
Oxalis corniculatum (Oxalidaceae)	*Amegilla* (*Megamegilla* sp. 1) (Apidae)	1
Psidium guajava (Myrtaceae)	*Apis mellifera* (Apidae)	3
Solanum nigrum (Solanaceae)	*Ceratina* sp. (Apidae)	1
Thunbergia alata (Acanthaceae)	*Ceratina* sp. 3 (Apidae)	1

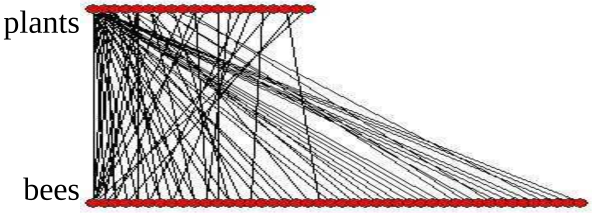
Appendix 3.7:

Forest Edge: A network approach to plant-bee mutualisms in the different seasons. Every red dot indicates a bee or plant species. A bee and a plant interact, if there is a qualitative link (black line) between them; bees and plants are ordered after the number of interaction partners and the number of interactions with their partners. Thus, generalist interaction partners are found on the left, specialists on the right.

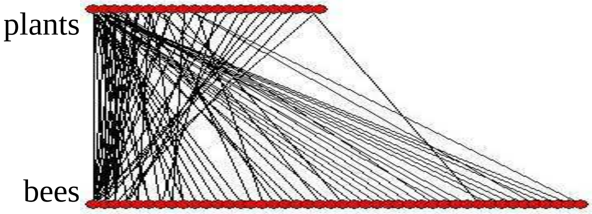
Forest Edge



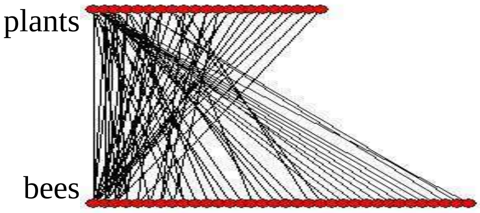
Longrain Season



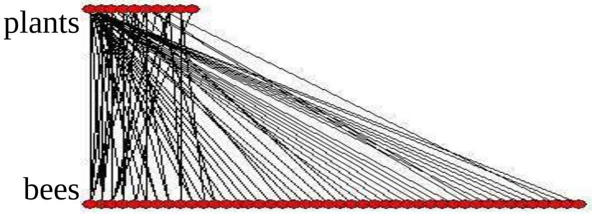
Colddry Season



Shortrain Season



Dry Season



Appendix 3.8:

Bee species and their interaction partners in the forest; reflecting the order of the pollination network analysis (Figure 3)

bee-species	plant species	Number recorded interactions
Apis mellifera (Apidae)	*Justicia flava* (Acanthaceae)	31
	Lantana camara (Verbenaceae)	8
	Harungana madagascariensis (Clusiaceae)	5
	Psidium guajava (Myrtaceae)	4
	Maesa lanceolata (Maesaceae)	4
	Asystasia gangetica (Acanthaceae)	2
	Justicia calyculata (Acanthaceae)	2
	Ageratum conyzoides (Asteraceae)	2
	Vernonia auriculifera (Asteraceae)	1
	Pollia condensator (Commelinaceae)	1
	Galinsoga parviflora (Asteraceae)	1
Ceratina sp. (Apidae)	*Justicia flava* (Acanthaceae)	2
	Asystasia gangetica (Acanthaceae)	1
	Rubus friesiorum (Rosaceae)	1
Halictidae	*Justicia flava* (Acanthaceae)	2
	Asystasia gangetica (Acanthaceae)	1
	Solanum mauritianum (Solanaceae)	2
Xylocopa melissa (Apidae)	*Justicia flava* (Acanthaceae)	19
	Acanthus pubescens (Acanthaceae)	2
Meliponula bocandei (Apidae)	*Lantana camara* (Verbenaceae)	1
	Rubus friesiorum (Rosaceae)	1
Xylocopa nigrita (Apidae)	*Justicia flava* (Acanthaceae)	1
	Desmodium repandum (Fabaceae)	1
Amegilla fallax (Apidae)	*Justicia flava* (Acanthaceae)	1
	Desmodium repandum (Fabaceae)	1
Lasioglossum sp. (Halictidae)	*Solanum mauritianum* (Solanaceae)	1
	Triumfetta rhomboidea (Tiliaceae)	1
Xylocopa calens (Apidae)	*Justicia flava* (Acanthaceae)	6
Megachile bituberculata (Megachilidae)	*Justicia flava* (Acanthaceae)	5
Megachilidae	*Justicia flava* (Acanthaceae)	6
Megachile felina (Megachilidae)	*Justicia flava* (Acanthaceae)	3
Xylocopa flavorufa (Apidae)	*Acanthus pubescens* (Acanthaceae)	1
Megachile torrida (Megachilidae)	*Justicia flava* (Acanthaceae)	3
Thyreus pictus (Apidae)	*Justicia flava* (Acanthaceae)	3
Xylocopa (*Kortosoma* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	3
Xylocopa carinata (Apidae)	*Justicia flava* (Acanthaceae)	2
Amegilla mimadvena (Apidae)	*Justicia flava* (Acanthaceae)	2
Ceratina (*Pithitis*) *nasalis* (Apidae)	*Justicia flava* (Acanthaceae)	2
Lasioglossum (*Sellalictus* sp.) (Halictidae)	*Justicia flava* (Acanthaceae)	1
Megachile ciactacombusta (Megachilidae)	*Justicia flava* (Acanthaceae)	2
Meliponula lendliana (Apidae)	*Justicia striata* (Acanthaceae)	2
Thyreus calceata (Apidae)	*Justicia flava* (Acanthaceae)	2
Thyreus interruptus (Apidae)	*Justicia flava* (Acanthaceae)	2
Xylocopa imitator (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla (*Megamegilla* sp. 1) (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla acraensis (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla aff *langi* (Apidae)	*Justicia flava* (Acanthaceae)	1
Amegilla cornuta (Apidae)	*Justicia flava* (Acanthaceae)	1

Braunsapis sp. (Apidae)	*Justicia flava* (Acanthaceae)	1
Ceratina viridis (Apidae)	*Justicia flava* (Acanthaceae)	1
Halictus (*Seladonia* sp. 1) (Halictidae)	*Psidium guajava*	1
Heriades sp. (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Lasioglossum (*Sellalictus* sp. 2) (Halictidae)	*Lantana camara*	1
Lipotriches aff. *welwitschii* (Halictidae)	*Psidium guajava*	1
Megachile dariensis (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile decemsignata (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile ianthoptera (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile niveicauda (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Megachile rufipes (Megachilidae)	*Justicia flava* (Acanthaceae)	1
Patellapis sp. 2 (Halictidae)	*Justicia flava* (Acanthaceae)	1
Thrinchostoma sp (Halictidae)	*Asystasia gangetica* (Acanthaceae)	1
Thrinchostoma torridum (Halictidae)	*Justicia flava* (Acanthaceae)	1
Thyreus sp (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa (*Xylomellisa* sp. 1) (Apidae)	*Acanthus pubescens* (Acanthaceae)	1
Xylocopa bouyssoui (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa erythrina (Apidae)	*Acanthus pubescens* (Acanthaceae)	1
Xylocopa hottentotta (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa inconstans (Apidae)	*Justicia flava* (Acanthaceae)	1
Xylocopa scioensis (Apidae)	*Justicia flava* (Acanthaceae)	1

Appendix 3.9:

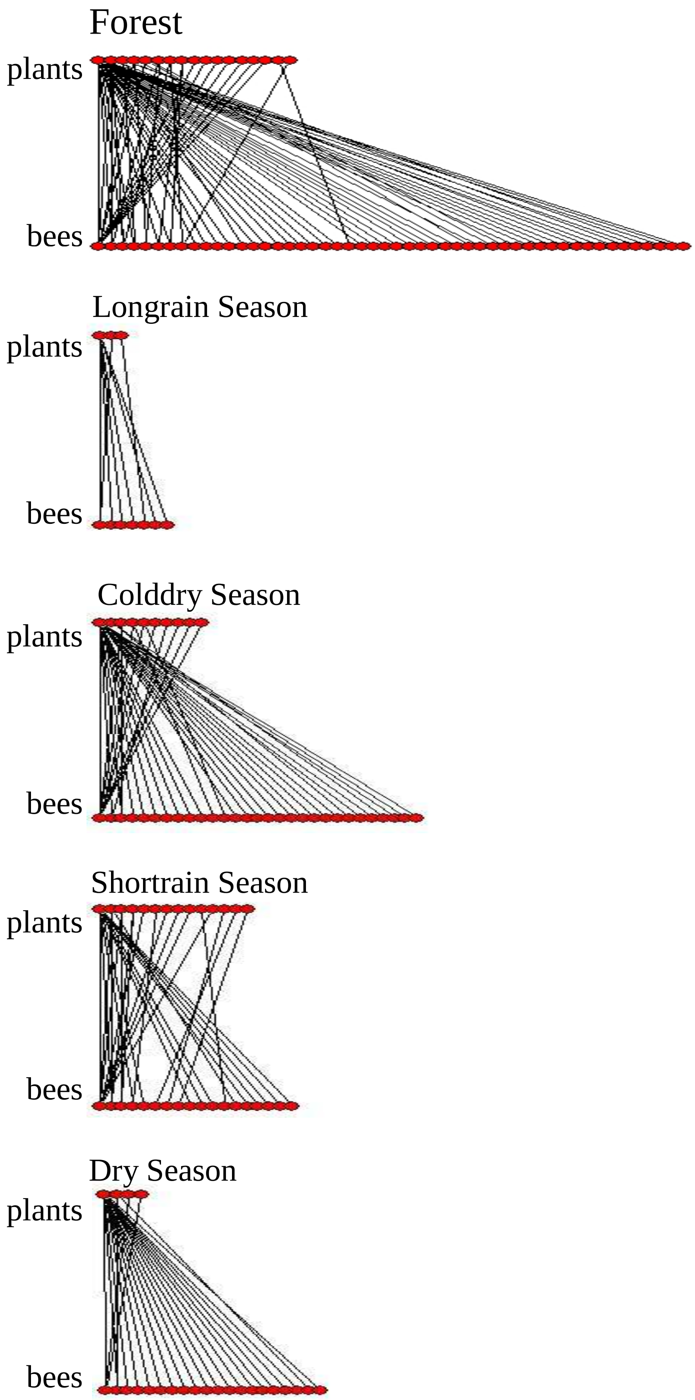
Plant species and their interaction partners in the forest; reflecting the order of the pollination network analysis (Figure 3)

plant species	bee-species	Number recorded interactions
Justicia flava (Acanthaceae)	*Apis mellifera* (Apidae)	31
	Ceratina sp. (Apidae)	2
	Halictidae	2
	Xylocopa melissa (Apidae)	19
	Xylocopa nigrita (Apidae)	1
	Amegilla fallax (Apidae)	1
	Xylocopa calens (Apidae)	6
	Megachile bituberculata (Megachilidae)	5
	Megachilidae	6
	Megachile felina (Megachilidae)	3
	Megachile torrida (Megachilidae)	3
	Thyreus pictus (Apidae)	3
	Xylocopa (*Kortosoma* sp. 1) (Apidae)	3
	Xylocopa carinata (Apidae)	2
	Amegilla mimadvena (Apidae)	2
	Ceratina (*Pithitis*) *nasalis* (Apidae)	2
	Lasioglossum (*Sellalictus* sp.) (Halictidae)	1
	Megachile ciactacombusta (Megachilidae)	2
	Thyreus calceata (Apidae)	2
	Thyreus interruptus (Apidae)	2
	Xylocopa imitator (Apidae)	1
	Amegilla (*Megamegilla* sp. 1)	1
	Amegilla acraensis (Apidae)	1
	Amegilla aff. *langi* (Apidae)	1
	Amegilla cornuta (Apidae)	1
	Braunsapis sp. (Apidae)	1
	Ceratina viridis (Apidae)	1
	Heriades sp. (Megachilidae)	1
	Megachile dariensis (Megachilidae)	1
	Megachile decemsignata (Megachilidae)	1
	Megachile ianthoptera (Megachilidae)	1
	Megachile niveicauda (Megachilidae)	1
	Megachile rufipes (Megachilidae)	1
	Patellapis sp. 2 (Halictidae)	1
	Thrinchostoma torridum (Halictidae)	1
	Thyreus sp (Apidae)	1
	Xylocopa bouyssoui (Apidae)	1
	Xylocopa hottentotta (Apidae)	1
	Xylocopa inconstans (Apidae)	1
	Xylocopa scioensis (Apidae)	1
Asystasia gangetica (Acanthaceae)	*Apis mellifera* (Apidae)	2
	Ceratina sp. (Apidae)	1
	Halictidae	1
	Thrinchostoma sp. (Halictidae)	1
Acanthus pubescens (Acanthaceae)	*Xylocopa melissa* (Apidae)	2
	Xylocopa flavorufa (Apidae)	1
	Xylocopa (*Xylomellisa* sp. 1) (Apidae)	1
	Xylocopa erythrina (Apidae)	1
Lantana camara (Verbenaceae)	*Apis mellifera* (Apidae)	8

	Meliponula bocandei (Apidae)	1
	Lasioglossum (*Sellalictus* sp. 2) (Halictidae)	1
Psidium guajava (Myrtaceae)	*Apis mellifera* (Apidae)	4
	Halictus (*Seladonia* sp. 1) (Halictidae)	1
	Lipotriches aff *welwitschii* (Halictidae)	1
Rubus friesiorum (Rosaceae)	*Ceratina* sp. (Apidae)	1
	Meliponula bocandei (Apidae)	1
Solanum mauritianum (Solanaceae)	Halictidae	2
	Lasioglossum sp. (Halictidae)	1
Desmodium repandum (Fabaceae)	*Xylocopa nigrita* (Apidae)	1
	Amegilla fallax (Apidae)	1
Harungana madagascariensis (Clusiaceae)	*Apis mellifera* (Apidae)	5
Maesa lanceolata (Maesaceae)	*Apis mellifera* (Apidae)	4
Vernonia auriculifera (Asteraceae)	*Apis mellifera* (Apidae)	1
Justicia calyculata (Acanthaceae)	*Apis mellifera* (Apidae)	2
Pollia condensator (Commelinaceae)	*Apis mellifera* (Apidae)	1
Ageratum conyzoides (Asteraceae)	*Apis mellifera* (Apidae)	2
Galinsoga parviflora (Asteraceae)	*Apis mellifera* (Apidae)	1
Justicia striata (Acanthaceae)	*Meliponula lendliana* (Apidae)	2
Triumfetta rhomboidea (Tiliaceae)	*Lasioglossum* sp. (Halictidae)	1

Appendix 3.10:

Forest: A network approach to plant-bee mutualisms in the different seasons. Every red dot indicates a bee or plant species. A bee and a plant interact, if there is a qualitative link (black line) between them; bees and plants are ordered after the number of interaction partners and the number of interactions with their partners. Thus, generalist interaction partners are found on the left, specialists on the right.



Appendix 4.1:

Bee species visiting the flowers of *Justicia flava*; in the field small species were grouped into 4 groups

Bee Family	Bee species	observation groups
Apidae	*Amegilla* aff. *vivida*	
	Amegilla acraensis	
	Amegilla aff. *langi*	
	Amegilla albigena	
	Amegilla albocaudata	
	Amegilla caelestina	
	Amegilla calens	
	Amegilla fallax	
	Amegilla mimadvena	
	Anthophora aff. *vegtita*	
	Apis mellifera	
	Braunapis angolensis	*Braunsapis*
	Braunsapis foveata	*Braunsapis*
	Braunsapis langenburgensis	*Braunsapis*
	Braunsapis leptozonia	*Braunsapis*
	Braunsapis lyrata	*Braunsapis*
	Ceratina ericia	*Ceratina*
	Ceratina moerenhouti	*Ceratina*
	Ceratina sp. 2	*Ceratina*
	Ceratina sp. 3	*Ceratina*
	Ceratina sp. 6	*Ceratina*
	Ceratina sp. 8	*Ceratina*
	Ceratina viridis	*Ceratina*
	Ctenoplectra antinorii	
	Ctenoplectra polita	
	Ctenoplectra terminalis	
	Pleibena hildebrandtii	small bee
	Tetraloniella katagensis	small bee
	Thyreus calceatus	
	Thyreus interruptus	
	Thyreus pictus	
	Thyreus vachali	
	Xylocopa albifrons	
	Xylocopa bouyssoui	
	Xylocopa calens	
	Xylocopa erythrina	
	Xylocopa hottentotta	
	Xylocopa inconstans	
	Xylocopa melissa	
	Xylocopa nigrita	
	Xylocopa scioensis	
	Xylocopa torrida	
Colletidae	*Hylaeus* sp. 1	small bee
Halictidae	*Halictus* (*Seladonia*) sp. 1	Halictid
	Halictus (*Seladonia*) sp. 2	Halictid
	Nomia (*Leuconomia*) sp. 1	
	Nomia (*Leuconomia*) sp. 2	
	Nomia theryi	
	Nomia viridiciacta	

	Patellapis (*Zonalictus*) sp. 2	Halictid
	Patellapis sp.	Halictid
	Systropha sp.	
Megachilidae	*Anthidium* sp.	
	Euaspis abdominalis	
	Euaspis erythros	
	Megachile bituberculata	
	Megachile dariensis	
	Megachile felina	
	Megachile ianthoptera	
	Megachile niveicauda	
	Megachile rufipes	
	Megachile torrida	
	Pachyanthidium bengalense	
	Pseudanthidium (*Microanthidium*) sp. 3	

Appendix 5.1:

Distances (in metres) between the study sites

		farmland					edge					forest			
		Buy C	Buy D	Kabr B	Kabr D	Kabr E	Buy A	Buy E	Buy F	Lus B	U Camp	Buy Hill	Camp A	Map A	Sal A
forest	Sal B	2643	2575	4532	4296	3985	2490	3277	3968	3445	2557	1697	2407	2321	373
	Sal A	2332	2324	4206	3957	3676	2222	2916	3596	3082	2193	1331	2055	1949	
	Map A	1215	1729	2595	2258	2257	1547	1061	1647	1378	421	661	585		
	Camp A	630	1170	2203	1918	1773	990	898	1716	1827	295	762			
	Buy Hill	1223	1524	2964	2678	2508	1356	1587	2285	1987	863				
edge	U Camp	869	1447	2190	1867	1837	1270	724	1470	1537					
	Lus B	2379	2979	2936	2535	2902	2805	1508	1211						
	Buy F	1992	2599	1809	1413	1943	2462	884							
	Buy E	1109	1721	1592	1224	1413	1580								
	Buy A	471	182	2182	2058	1562									
farmland	Kabr E	1345	1558	657	728										
	Kabr D	1709	2105	401											
	Kabr B	1899	2197												
	Buy D	621													

Appendix 5.2:
Bee species visiting the flowers of *Justicia flava*; in the field small species were grouped into 4 groups

Bee Family	Bee species	observation groups
Apidae	*Amegilla* aff. *vivida*	
	Amegilla acraensis	
	Amegilla aff. *langi*	
	Amegilla albigena	
	Amegilla albocaudata	
	Amegilla caelestina	
	Amegilla calens	
	Amegilla fallax	
	Amegilla mimadvena	
	Anthophora aff. *vegtita*	
	Apis mellifera	
	Braunapis angolensis	Braunsapis
	Braunsapis foveata	Braunsapis
	Braunsapis langenburgensis	Braunsapis
	Braunsapis leptozonia	Braunsapis
	Braunsapis lyrata	Braunsapis
	Ceratina ericia	Ceratina
	Ceratina moerenhouti	Ceratina
	Ceratina sp. 2	Ceratina
	Ceratina sp. 3	Ceratina
	Ceratina sp. 6	Ceratina
	Ceratina sp. 8	Ceratina
	Ceratina viridis	Ceratina
	Ctenoplectra antinorii	
	Ctenoplectra polita	
	Ctenoplectra terminalis	
	Pleibena hildebrandtii	small bee
	Tetraloniella katagensis	small bee
	Thyreus calceatus	
	Thyreus interruptus	
	Thyreus pictus	
	Thyreus vachali	
	Xylocopa albifrons	
	Xylocopa bouyssoui	
	Xylocopa calens	
	Xylocopa erythrina	
	Xylocopa hottentotta	
	Xylocopa inconstans	
	Xylocopa melissa	
	Xylocopa nigrita	
	Xylocopa scioensis	
	Xylocopa torrida	
Colletidae	*Hylaeus* sp.1	small bee
Halictidae	*Halictus* (*Seladonia*) sp. 1	Halictid
	Halictus (*Seladonia*) sp. 2	Halictid
	Nomia (*Leuconomia*) sp. 1	
	Nomia (*Leuconomia*) sp. 2	
	Nomia theryi	
	Nomia viridiciacta	

	Patellapis (*Zonalictus*) sp. 2	Halictid
	Patellapis sp.	Halictid
	Systropha sp.	
Megachilidae	*Anthidium* sp.	
	Euaspis abdominalis	
	Euaspis erythros	
	Megachile bituberculata	
	Megachile dariensis	
	Megachile felina	
	Megachile ianthoptera	
	Megachile niveicauda	
	Megachile rufipes	
	Megachile torrida	
	Pachyanthidium bengalense	
	Pseudanthidium (*Microanthidium*) sp. 3	

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Ungalijua alacho nyuki, usigalionja asali.

Had you known what bees eat, you would not have tasted the honey.
Swahili saying

CURRICULUM VITAE OF MELANIE HAGEN

Personal information

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Place of Birth: Mettmann (Germany)

School education

1983-1987	Alexander-von-Humboldt-Grundschule Monheim (Elementary School)
1987-1996	Otto-Hahn-Gymnasium Monheim (Secondary school) *Degree: Allgemeine Hochschulreife*

Academic education

1996-2003	Undergraduate studies in Biology at the University of Bonn (Rheinische Friedrich-Wilhelms-Universität Bonn), with a specialisation on Ecology, Conservation Biology and Evolution
2002-2003	Master thesis: "*Justicia flava* (Acanthaceae) and its flower visitors: Differences in pollination efficiency" (4 month of fieldwork in Kenya) at the Alexander Koenig Research Institute and Museum of Zoology, Bonn supervised by Prof. Dr. C.M. Naumann & Dr. M. Kraemer *Degree: Diplom-Biologin (~Master)*
since June 2004	Phd-Project: " Composition, spatial heterogeneity and seasonal turnover in Plant-Pollinator communities in an Agriculture-Forest-Mosaic " at the University of Bielefeld, Germany

Experiences

1998	Trainee at the 'Biologische Station Urdenbacher Kämpe e.V.' (station for Nature Conservation, Germany), area of responsibility: mapping and digitizing of vegetation (GIS ARC View)
2001	Trainee at the 'Bundesamt für Naturschutz' (Federal Agency for the Conservation of Nature), area of responsibility: drawing up maps of endangered mosses of Germany
2002-2004	Assistance at the Alexander Koenig Research Institute and Museum of Zoology, Bonn; area of responsibility: preparation of a pollen-catalogue of plants of the Kakamega Forest using a scanning electron microscope; identification and sorting of arthropods to family-level

2003	Assistance in the University Course “Taxonomy and Ecology of Bees and Wasps (with Dr. Inge Bischoff), University of Bonn
2003-2004	Participation in a project dealing with the impact of relative plant density in a linear population (along the river Rhein) on behaviour of flower-visitors and fruitset of *Solidago canadensis* (Asteraceae)
2003-2004	Participation in a project in Kakamega Forest (Kenya) dealing with the competitive influence of neighbouring plant-species of the genus *Dissotis* (Melastomataceae) on the visiting pollinators and the current seedset, influence of stingless bees (*Meliponura*) on the pollination-ability of *Xylocopa*-bees
2006	Assistance in the University Course “Bee Taxonomy and Pollination Ecology” (with Dr. Manfred Kraemer & Dr. Connal Eardley), National Museums of Kenya, Nairobi

Further qualifications – Field trips

2002	June – September: Data collection for the diploma thesis in Kakamega Forest, Kenya
2003	Field assistance for Bayer-Cropscience, area of responsibility: Collecting and determining arthropods (pit fall traps, malaise traps, car-netting, fogging) in Malalbergo, Italy
2003	Field assistance for Bayer-Cropscience, area of responsibility: trapping and radio tracking of small birds and mammals in Bavaria, Germany
2003	October – December: Data collection for the *Dissotis*-Project
2004	Field assistance for Bayer-Cropscience, area of responsibility: trapping and radio tracking of small mammals in Niederösterreich, Austria
2004-2006	Four fieldtrips (in total 12 months) to Kakamega Forest, Kenya; data collection for the PhD-Thesis

Publications:

Frahm J.-P., Ahmed J., Hagen M., Peles M. 2000. Revision der Gattung *Rhabdoweisia* (Musci, Dicranaceae). Tropical Bryology 18: 161-172.

Hagen, M.; Kraemer, M. 2006. Einfluss der Landschafts-Strukturierung auf Pflanze-Bestäuber Interaktionen in einem ostafrikanischen Wald-Agrarland Mosaik. In: Korn, H. & Veit. U. (eds.). Treffpunkt Biologische Vielfalt VI. 63-68.

Grants and Scholarships

2002	DAAD Research Scholarship, from the German Academic Exchange Service to conduct Diplom thesis research in Kenya

2008	Scholarship of the Equal Opportunities Commission of the University of Bielefeld to visit the 2008 Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)

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HAGEN, M.; KRAEMER, M. 2003. *Justicia flava* (Acanthaceae) and its flower visitors: Differences in pollination efficiency. 16th Annual meeting of the German Society of Tropical Ecology, February 19.-22., Rostock, Germany (poster).

HAGEN, M. 2004. Influence of landscape structure on plant-pollinator interactions in an East-African Agriculture-Forest Mosaic. Pollinator-workshop in the National Museums of Kenya, Nairobi, Kenya (talk).

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GIKUNGU, M.; HAGEN, M.; KRAEMER, M. 2008. An overview of pollinator studies in Kenya. 9th meeting of the Conference of the Parties (COP9), May 19.-30., Bonn, Germany (poster).

HAGEN, M.; KRAEMER, M. 2008. Spatio-temporal variation in pollination networks. Annual meeting of the Association for Tropical Biology and Conservation with The Society for Tropical Ecology June 9.-13., Paramaribo, Suriname (talk).

Bielefeld, 2008-09-29

ERKLÄRUNG

Ich versichere, dass ich diese Arbeit selbständig verfasst, keine anderen Quellen und Hilfsmittel als die angegebenen benutzt und die Stellen der Arbeit, die anderenWerken dem Wortlaut oder Sinn nach entnommen sind, kenntlich gemacht habe.
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Bielefeld, den 29. September 2008

Melanie Hagen