

Forest fragmentation and plant-pollinator interactions in Western Kenya

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Meinen Eltern

In Andenken an

Prof. Dr. Clas M. Naumann

“Biodiversity benefits people through more than just its contribution to material welfare and livelihoods. Biodiversity contributes to security, resiliency, social relations, health, and freedom of choices and actions.”
(WRI, 2005)

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1. Biodiversity in tropical forests and pollination

The Convention on Biological Diversity of Rio de Janeiro (Brazil) identified the “*importance of biological diversity for evolution and for maintaining life sustaining systems of the biosphere*” and the “*general lack of information and knowledge regarding biological diversity*”. In addition, the signatory states stressed “*that biological diversity is being significantly reduced by certain human activities*” (CBD, 1992).

Historically, scientists recognized the contrast between the tremendous diversity of tropical plants and animals and the much lower diversity of plants and animals in temperate regions since the mid-nineteenth century (Bates, 1864; Wallace, 1878; Huston, 1994). The increase of the average species richness moving from high to low latitudes has already been documented for a wide spectrum of taxonomic groups (Gaston, 2000). After fogging the canopies of tropical rain forests, Erwin (1982) corrected conservative estimations of about 2 million animal species living on our planet “very optimistically” (Freund, 2004) to a plausible upper limit of 30 million species including all rain forests in the world due to a high amount of previously unknown arthropod species in his samples.

Myers et al. (2000) identified plant and vertebrate “*biodiversity hotspots*”. Regarding the 300,000 plants species known world wide, seven of the top ten endemic plant hotspots include rain forests (Myers et al., 2000). This observation led the authors to describe tropical forests as “*major wilderness areas*”.

In addition, Wilson (1988) not only called rain forests “*centres of diversity*”, but also emphasized two principal reasons for biologists and conservationists to focus increasing attention on tropical rain forests:

“First, although these habitats cover only 7% of the Earth’s land surface, they contain more than half the species in the entire world biota. Second, the forests are being destroyed so rapidly that they will mostly disappear within the next century, taking with them hundreds of thousands of species into extinction.”
(Wilson, 1988)

It is well-known that the increase in human population forced a dramatic change upon the natural environment. The high diverse rain forests are under enormous anthropogenic pressure leading to a severe biodiversity decline due to habitat loss (Myers, 1988; Heywood, 1995; Pimm et al., 1995). Unfortunately, this pressure results especially from the fact that surrounding areas of tropical rain forests are densely populated in countries with very high population growth rates (Blackett, 1994; Tattersfield et al., 2001). The increased anthropogenic use of land is one of the most important drivers of environmental change (Sala et al., 2000). Therefore, degradation transforms primary to secondary forest systems. Furthermore, close and widespread forests split up into forest fragments and will be deforested afterwards (Whitmore, 1997; Laurance et al., 2000). Up to now, nearly one quarter of the tropical rain forest biome has been fragmented or removed by humans (Wade et al., 2003).

“The current massive degradation of habitat and extinction of many of the Earth’s biota is unprecedented and is taking place on a catastrophically short timescale.”
(Novacek & Cleland, 2001)

Fragmentation of natural habitats not only affects the distribution and the abundance of organisms, it may also disturb the important biological processes that maintain biodiversity and that are of high importance for the functioning and the long-term existence of ecosystems (Harrison & Bruna, 1999; Naeem et al., 1999; Chapin et al., 2000; Kraemer & Bergsdorf, 2001).

Janzen (1974) already remarked in the early seventies:

“What escapes the eye, however, is much more insidious kind of extinction: the extinction of ecological interactions. Many of the remaining participants of these interactions will probably hold on for many years, but they constitute little more than haphazard, semi-self-sustaining zoo and botanical garden.”

Consequences upon essential ecosystem processes like seed dispersal (Peres, 2000; Wright et al., 2000) and regeneration (Laurance et al., 2000; Pacheco & Simonetti, 2000; Wright et al., 2000) are expected. Furthermore, Kevan (1975) stressed that *“the often unknown but undoubtedly important interrelationships of pollinators and plants constitute a serious void”* in both agricultural and natural communities.

It is generally accepted that pollination is a major step in the life-history of most flowering plants and therefore it is of high significance to the organization of plant communities and to the long-term maintenance of whole vegetational units and its capability for regeneration (Buchmann & Nabhan, 1996). Almost 100 percent of the flowering plant species in tropical forests are pollinated by animals, with bees being among the most important pollinators (Roubik, 1989; Neff & Simpson, 1993; Kraemer & Bergsdorf, 2001). Consequently, pollination is an essential ecosystem service (Fig.1).

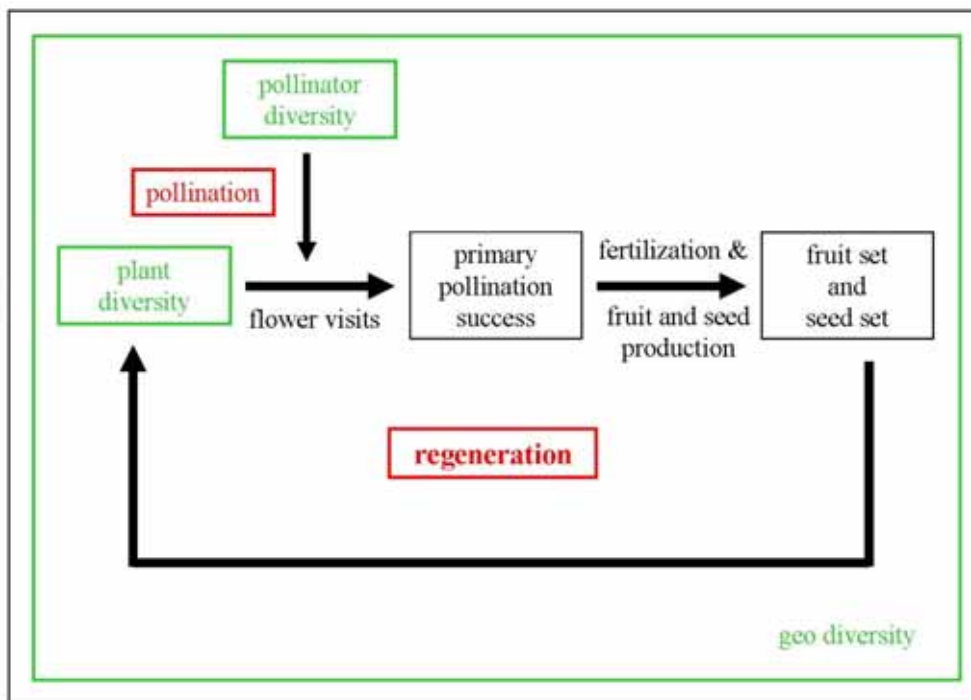


Fig. 1: Linking Diversity and Ecosystem Processes (Kraemer et al., 2001)

In consideration of these ecosystemic coherences, Buchmann and Nabhan (1996) stressed the dire need of pollination conservation and established the “Forgotten Pollinators Campaign”. In the same year, the Third Conference of the Parties (COP 3)

of the Convention on Biological Diversity (CBD) gave pollinators priority for publishing case studies in its biodiversity programme (CBD, 1996). This stimulated global interest in pollination conservation, and the first subsequent major activity was an international symposium in Sao Paulo, Brazil (1998). This resulted in the Sao Paulo Declaration (IPI, 1999), which called for an international pollinator initiative and documented many activities required for pollinator conservation.

Moreover, because of the fact that a lot of crops also depend on pollinators, the African Pollinator Initiative (API), founded in 1999, stressed the need for deeper understanding of plant-pollinator interactions both in agricultural and natural ecosystems “*for sustainable livelihoods and the conservation of biological diversity in Africa*” (API, 2003). But Roger et al. (2004) still identified a huge lack of basic knowledge and information concerning pollination relationships, especially focusing on Africa in general and concerning fragmented rain forest systems in particular.

2. Pollination and fragmentation

It is largely accepted that fragmentation of natural habitats is one of the greatest threats to terrestrial biodiversity worldwide (Jennersten, 1988; Rathcke & Jules, 1993; Turner, 1996). Habitat fragmentation can affect animal and plant populations, but also essential ecosystem processes, like plant-pollinator interactions (Aizen et al., 2002). In theory (Fig. 2), a reduction in population size and an increase in isolation due to fragmentation may lead to limited gene flow, increased inbreeding, loss of genetic variation, decreased individual fitness, and consequently result in an increased risk of population extinction (Murcia, 1995; Jules & Rathcke, 1999; Cunningham, 2000a; 2000b; Jacquemyn et al., 2002; Ghazoul, 2005).

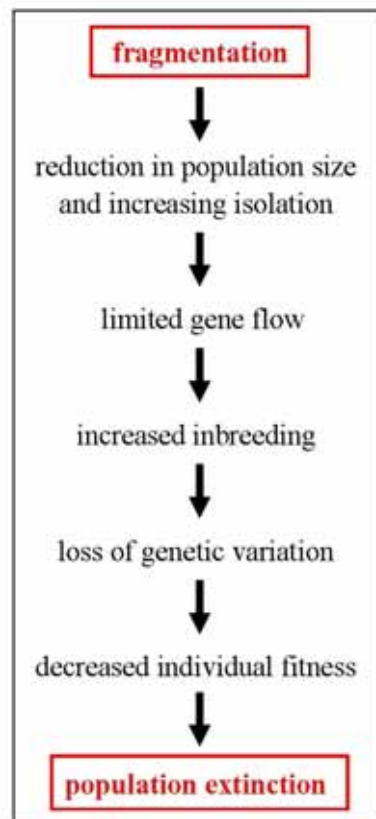


Fig. 2: Theory of fragmentation and extinction

Several studies appear to support this theory on different levels of pollination and seed dispersal (Jennersten, 1988; Aizen & Feinsinger, 1994b; Murcia, 1995; Didham et al., 1996; Kearns et al., 1998; Jules & Rathcke, 1999; Cunningham, 2000a; 2000b; Jacquemyn et al., 2002). But just a few studies actually quantified pollination success in habitat fragments (Ghazoul, 2005), especially in highly diverse and complex rain forest systems.

For the most part studies reported a decline in pollinator abundance as response to habitat fragmentation (Jennersten, 1988; Aizen & Feinsinger, 1994b; Liow et al., 2001; Lennartsson, 2002). In addition, limits to pollinator movement among patches were found (Steffan-Dewenter & Tschardt, 1999; Goverde et al., 2002). Therefore, fewer flower visits (Jennersten, 1988; LaMont et al., 1993; Schulke & Waser, 2001) and smaller pollen loads (Cunningham, 2000a) or poorer pollen quality (Severns, 2003)

were described in fragments. This might lead to limited pollen flow and increased inbreeding (Richards et al., 1999; Richards, 2000) resulting in progeny that is less fit (Agren, 1996), which among other reasons depresses reproductive success (Cunningham, 2000b).

Up to now, following the reviews conducted by Aizen et al. (2002) and Ghazoul (2005) about 40 important studies have been published, which either explicitly or implicitly dealt with the potential impact of fragmentation and/or patch sizes on plant reproductive ecology. In these reviews about 70 plant species were integrated. Only four of these studies were conducted in tropical rain forest remnants: (1) on an understory palm (*Calyptranthes ghiesbreghtiana* [Arecaceae]) and its pollen supply in Costa Rica (Cunningham, 1996); (2) on the tropical tree *Pithecellobium elegans* [Mimosaceae] and its genetic diversity and mating system in Costa Rica (Hall et al., 1996); (3) on the tropical forest tree *Symphonia globulifera* [Buttiferaceae] and its reproductive dominance in Costa Rica (Aldrich & Hamrick, 1998); and (4) on the tropical tree *Dinizia excelsa* [Fabaceae] and its pollen dispersal inside the Amazonian rain forest (Dick et al., 2003). In these studies no clear pattern of response became obvious. Cunningham (1996), Hall et al. (1996) and Dick et al. (2003) documented negative effects of smaller patch sizes on plant reproductive biology. In contrast to this, Aldrich & Hamrick (1998) found a higher reproductive output due to fragmentation.

Most of the fragmentation and/or patch sizes oriented studies in respect of forest habitats were conducted in non-rain forest systems. Also here, the authors reported about different consequences on pollination and reproductive success as a result of fragmentation processes: significant negative (Aizen & Feinsinger, 1994a; Nason & Hamrick, 1997; Ghazoul & McLeish, 2001; Rocha & Aguilar, 2001; Quesada et al., 2003), significant positive (Aizen & Feinsinger, 1994a) or non-significant (Aizen & Feinsinger, 1994a; Ghazoul & McLeish, 2001; Cascante et al., 2002) effects.

Regarding Africa, a large number of studies on pollination in general have been conducted in the floristically unique Cape region in South Africa. This could be assumed as the only region in Africa where pollination biology might be regarded as reasonably well studied (Rodger et al., 2004). But also here, studies on fragmentation and plant reproductive ecology are very rare.

3. Objectives

“*Chovya chovya humaliza buyu la asali*” –
“Dip after dip depletes a jar of honey”
(Kenyan saying)

This study was conducted due to the following reasons:

- a general lack of knowledge and a limited understanding of plant-pollinator interactions in fragmented landscapes (Steffan-Dewenter et al., 2006), in particular with respect to tropical forest systems (Aizen et al., 2002; Ghazoul, 2004)
- the reviewed papers showed substantial differences in certain aspects of the pollination biology between Africa and the rest of the world (Rodger et al., 2004)
- the urgent need of a better understanding of these crucial and highly complex ecological processes for a potential formulation of effective conservation protocols that could also facilitate the sustainable use of forests and forest resources (Ghazoul, 2004).

In this context this study focused on the following questions:

- Does the fragmentation of the Kakamega Forest affect different levels of pollination, such as visitation frequency, primary pollination success, seed and/or fruit set?
- Are general patterns visible inside the Kakamega main forest and its fragments regarding pollination levels and the different observed plant species?
- Do the observed rain forest plant species potentially show pollinator or pollen limitation at a forest fragment level in Kakamega Forest?
- Which abiotic and biotic factors have influences on the levels of pollination in Kakamega Forest?

4. Study area

“*Fuata nyuki ule asali*” –
 “Follow bees and get honey”
 (Kenyan saying)

4.1 Kakamega Forest and surrounding forest fragments

The field work was conducted at Kakamega Forest (between latitudes of 00°10’N and 00°21’N and longitudes of 34°47’E and 34°58’E), in Western Kenya at an altitude of 1,500 to 1,700m near the border with Uganda and about 50 km north of Lake Victoria (Fig. 3). It is situated in the Shinyalu Division of Kakamega District in the Western Province of Kenya.

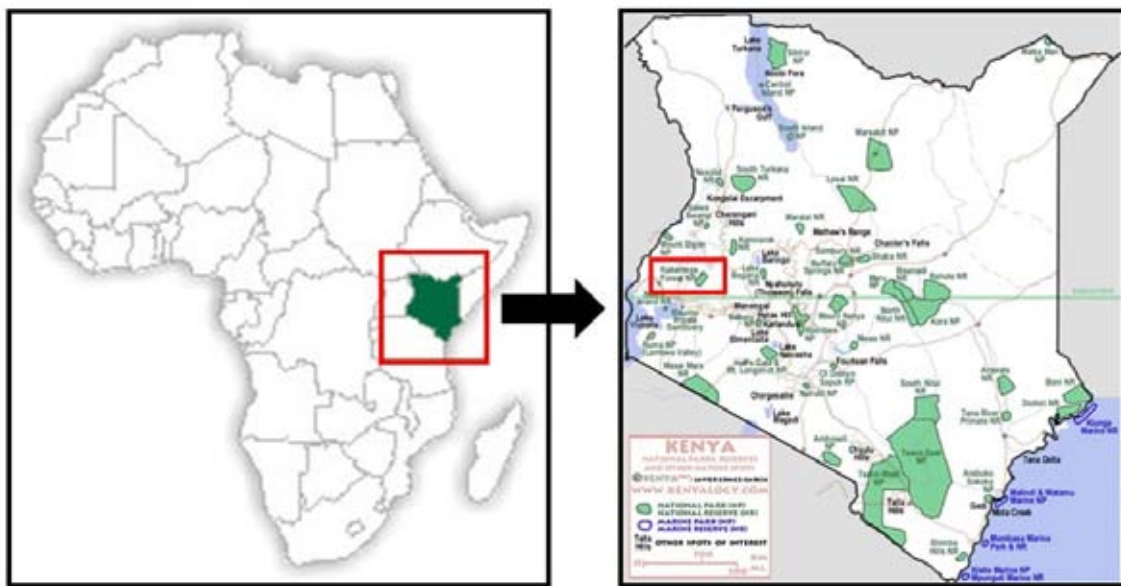


Fig. 3: Political map of Africa (inside the red box: Kenya); National Parks, Reserves and other nature spots (inside the red box: Kakamega Forest in Western Kenya)

The local Luyia community originally called the Kakamega area “Shieywe”, named after a sort of grass which was used for thatching huts in this region. Due to difficulties in communication between the British colonialists and the local chiefs the commissioner named the area Kakamega (Inhaji Analo, 2003).

Kakamega Forest is a mid-altitudinal tropical rain forest considered to be the easternmost remnant of the lowland Congo basin rain forests of Central Africa (Kokwaro, 1988; Sayer et al., 1992; Wass, 1995). Due to new vegetation surveys and according to Knapp (1973), Lind & Morrison (1974) and White (1983) Althof (2005) concluded that Kakamega Forest should be identified as a dry peripheral semi-evergreen Guineo-Congolian transitional rain forest related to the Congo basin.

Following the land cover classes of Lung & Schaab (2004), about 11,800 ha of “*near natural & old secondary fores*” and “*secondary fores*” still existed in the year 2001. However due to its location amidst the densest populated agricultural centre in the world with about 600 people per km² (Blackett, 1994; Tattersfield et al., 2001), Kakamega Forest has been continually exploited for many years (Kokwaro, 1988; Wass, 1995) and is now highly fragmented and disturbed (Fig. 4).

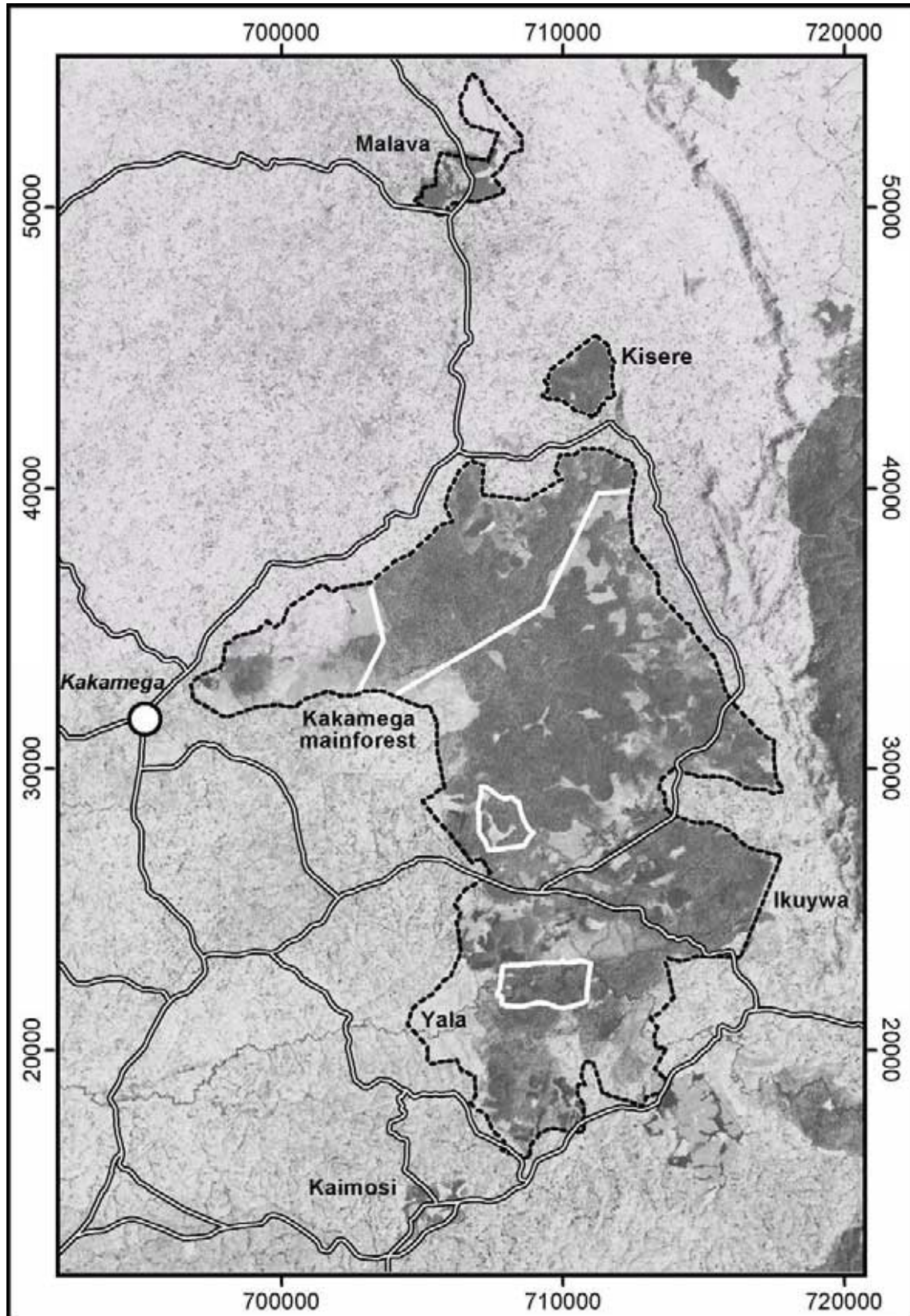


Fig. 4: Satellite image (channel 5 of Landsat 7 ETM+, 05 Feb 2001) of Kakamega main forest and its five fragments (Malava, Kisere, Ikuywa, Yala and Kaimosi) in Western Kenya with official forest boundaries gazetted in 1933 (dashed line) and official boundaries of National and Nature Reserves (white line). Coordinates in UTM 36 N. (G. Schaab, BIOTA E02)

A further increase of population density in the next decades with its linked anthropogenic pressure of harvesting and forest exploitation is most likely (Tsingalia, 1988; Cincotta et al., 2000).

Management history

Kakamega Forest was first gazetted as Trust Forest under proclamation No. 14 in 1933 and has since been managed by the Forest Department (FD). In 1964 it was declared to be a Central Forest (Blackett, 1994). Three small Nature Reserves, Isecheno, Kisere and Yala, were established and gazetted within the Forest Reserve in 1967 (Blackett, 1994). In 1986, the northern part of Kakamega called Buyangu together with the adjacent Kisere Forest was gazetted as Kakamega National Reserve and fell under management of the Kenya Wildlife Service (KWS). Today, Kakamega Forest is partly a Forest Reserve, partly Nature Reserve and partly National Reserve, and its management is under the authority of both, FD and KWS, on behalf of the state (Fig. 4) (Bleher et al., 2005).

Wass (1995) characterised the management aims and strategies as follows, the FD is intending “*to enhance conservation and protection of indigenous forest, to improve the production of timber and fuel wood and to establish a framework for long-term development forestry*” and the KWS would like “*to conserve, protect and sustainably manage the wildlife resources*”.

Climate and soil conditions

Annual rainfall in Kakamega Forest is 2007 mm (as averaged from FD records at Isecheno Forest Station from 1982 to 2001) and highly seasonal with a *rainy season* from April to November and a *short dry season* from December to March. The average monthly maximum temperature ranges from 18 to 29°C while the average monthly minimum temperature ranges from 4 to 21°C (Muriuki & Tsingalia, 1990). But, during field work between 2001 and 2003, a regular change of dry and wet season was not evident (Freund, 2004).

The dominant soil classes in Kakamega Forest are Ferrasols, Lixisols, Cambisols and Phaeozems. Most soils are deep to very deep on a flat to undulating terrain. Soil texture is predominantly clayey. All soils have low nutrient levels and range from very strongly acidic to slightly acidic (pH 4.5-6.5). Soils in the northern part of the forest are in more advanced stage of weathering as compared to the southern part with an exception of Isecheno soils. These factors may strongly limit plant growth (Musila et al., 2005).

Plant diversity

Kakamega Forest is a unique mixture of Guineo-Congolian and Afromontane species with most of the Guineo-Congolian species reaching their easternmost distribution limit. All in all, 397 species of 93 families were found in Kakamega Forest with the highest amount of species occurring in the disturbed areas with secondary forest (Buyangu hill). The more undisturbed forests in Southern Kakamega (Yala) are richer in different species than comparable areas in the Northern part (Kisere fragment and the protected area of the Colobus forest). All observed plant communities of Kakamega Forest were influenced by human activities in the last decades (Althof, 2005).

Animal diversity

The Kakamega Forest houses a large number of animals. With respect to primates you can find the Olive Baboon (*Papio anubis*), the Black and White Colobus (*Colobus guereza*), the Blue Monkey (*Cercopithecus mitis*), the Red-tailed Monkey

(*Cercopithecus ascanitus*) and the De Brazza's Monkey (*Cercopithecus neglectus*). In addition, there are numerous antelope species, the Bushbuck (*Tragelaphus scriptus*), the Blue Duiker (*Cephalophus monticola*), the Red Duiker (*Cephalophus harveyi*) and the Common Duiker (*Sylvicapra grimmia*).

With respect to reptiles and amphibians, the forest ranges among the richest areas in Kenya. Commonly encountered species include e.g. the Gaboon Viper (*Bitis gabonica*), the Rhinoceros Viper (*Bitis nasicornis*), the Forest Cobra (*Naja melanoleuca*), the Jameson's Mamba (*Dendroaspis jamesoni kaimosae*), and diverse tree frog species (*Hyperolius spec.*) (Köhler, 2004; Wagner, 2004).

The avifauna of the Kakamega Forest is a unique combination of central lowland and highland species. With more than 350 recorded species the diversity is very high (KIFCON, 1994) and over 200 species are forest dependants (Inhaji Analo, 2003).

The insect fauna of Kakamega Forest and its surrounding farmland is also greatly diverse, especially with regard to butterflies (Lepidoptera), of which more than 490 species or 55% of approximately 900 Kenyan species have been recognized so far (Kühne et al., 2004). In addition, a total number of 71 dragonfly species (Clausnitzer, 2004) have been recorded from the forest. With respect to bees, the probably most important group of pollinators, all in all about 230 species from four bee families were found by Gikungu (2006). The most dominant families were Apidae, Halictidae and Megachilidae; the family Colletidae was found to be very sparsely distributed. Furthermore, Gikungu (2006) described along a gradient a clear pattern of bee species richness, as well as bee abundance. The highest number was recorded in farmland followed by bushland and found to decrease with forest age in almost every family.

Anthropogenic impact

Kakamega Forest has been continually exploited for many years due to the high surrounding population pressure (Kokwaro, 1988; Wass, 1995). As a result, it lost about 20% in forest area over the past 30 years (Lung & Schaab, 2004).

Human impact – such as logging, paths, debarking, charcoal production and honey gathering – could be found in different forest parts, whereas selective logging occurs over the entire Kakamega Forest (Bleher et al., 2005). These disturbances have also been observed by Mutangah (1996), who stated the highest logging levels took place in the most southern part of the forest as well as along the western edge. Furthermore, Bleher et al. (2005) showed that the number of trees logged illegally in the last 20 years was significantly lower in forest parts managed by KWS and within highly protected National and Nature Reserves, respectively. The lowest logging levels were found in the northern Kakamega National Reserve, in central Ikuywa and Yala.

4.2 Study sites

The study sites were spread over the entire Kakamega Forest, inside the main forest fragment (subsequently called: main forest) and its surrounding forest fragments (subsequently called: forest fragments) (Table 1; Fig. 5).

Table 1: Study sites arranged from north to south

Main forest fragment	Surrounding forest fragments
Colobus trail	Malava Forest
Buyangu hill	Kisere Forest (North & South)
Salazar circuit I & II	Ikuywa Forest
Isecheno circuit (North & South)	Yala Forest
	Kaimosi Forest

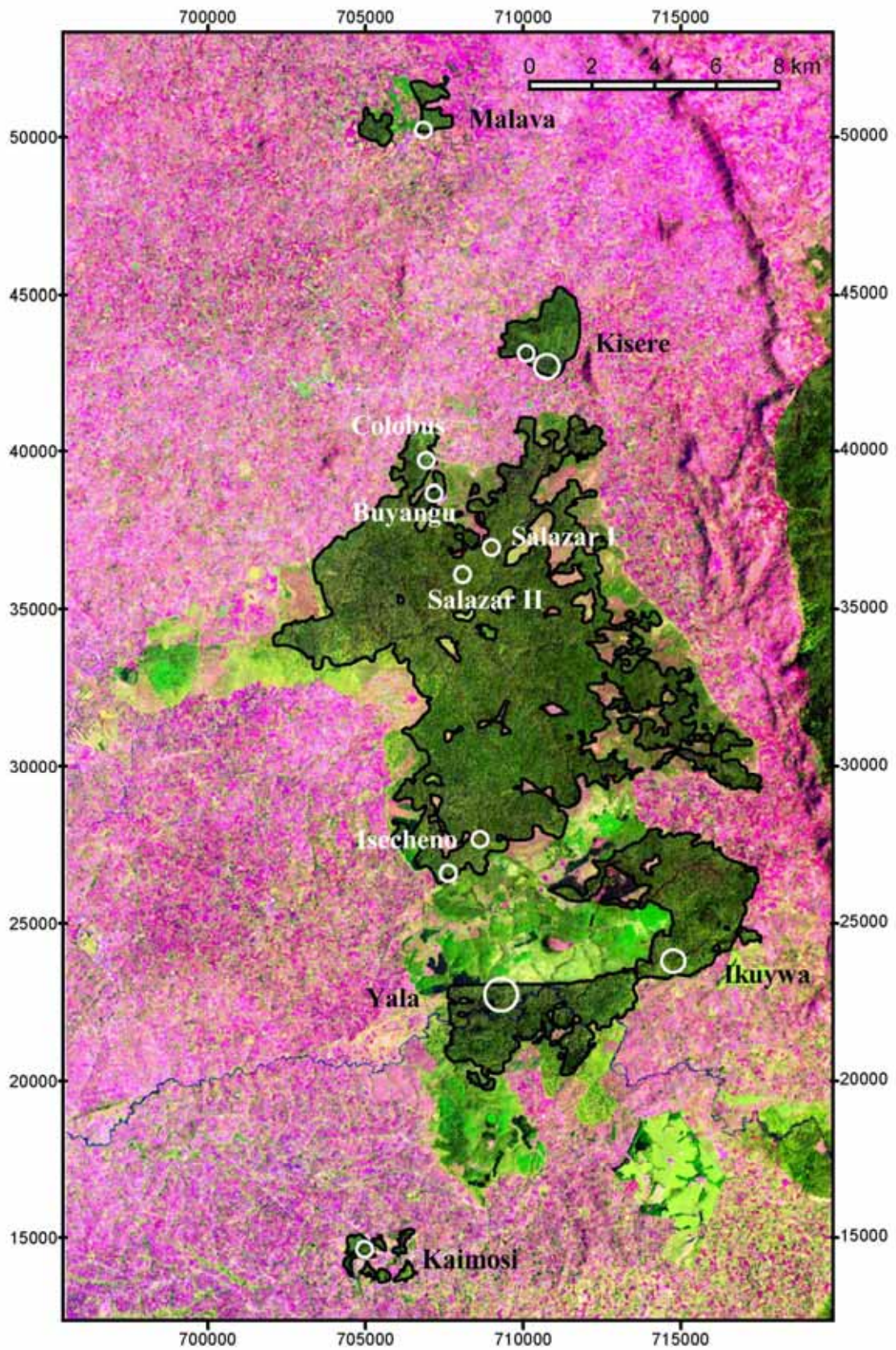


Fig. 5: Satellite image (channel 5 of Landsat 7 ETM+, 05 Feb 2001) of the Kakamega main forest (white scripture) and fragment (black scripture) study sites (white circles); Coordinates in UTM 36 N. (BIOTA E02, G. Schaab)

4.2.1 Main forest study sites

Colobus trail

Table 2: Characterization of the Colobus trail study site

Location	northern study site inside Kakamega Forest (Fig. 5)
Size	8,245 ha (Lung & Schaab, 2004)
Management regime	Kenya Wildlife Service (KWS)
Protection status	Nature Reserve
Disturbance history	<p>1913/16 map: one of the few areas of full forest at that date; from 1943: Kakamega Sawmill cut timber; from 1973 to the mid-1970's (reported by local people): Elgeyo Sawmill worked there (Mitchell, 2004)</p> <p>until 1989: some decrease in near-natural and secondary forest, especially along the edges of the forest glades and along the northern and eastern forest edge; afterwards: the trend reverses (bushland decrease in favour of secondary forest, hardly any agricultural land can be found in the glades anymore) (Lung & Schaab, 2004)</p> <p>lowest logging levels were found in the northern Kakamega National and Nature Reserve (Bleher et al., 2005)</p>
Cut trees	5.2 per ha (Bleher et al., 2005)
Paths	3 per ha (Bleher et al., 2005)
Humidity	59.0 % (Althof, 2005)
Soil classification	Rhodic Ferrasols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.6; C/N ratio: 10; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 140; $[\text{Ca}^{++}]$: 80; $[\text{Mg}^{++}]$: 19.4 (Musila et al., 2005)
Plant community	<i>Deinbollia kilimandscharica</i> – <i>Markhamia lutea</i> (Althof, 2005)
Succession stage	middle-aged secondary (Althof, 2005)
No. of plant species	135 (Evenness via Shannon-Wiener: 0.754) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	87.5 % (100 m buffer); 62.1 % (500 m buffer); 59.51 % (1,000 m buffer); 33.91 % (2,000 m buffer) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> ; <i>Acanthus eminens</i> ; <i>Heinsenya diervilleoides</i> ; <i>Dracaena fragrans</i>

Buyangu hill

Table 3: Characterization of the Buyangu hill study site

Location	northern study site inside Kakamega Forest (Fig. 5)
Size	8,245 ha (Lung & Schaab, 2004)
Management regime	Kenya Wildlife Service (KWS)
Protection status	Nature Reserve
Disturbance history	<p>1931 (old people remember): families lived on Buyangu hill before the forest boundary was altered and used to cut thatching grass there; in the mid-1970's: Elgeyo Sawmill cut timber from Buyangu hill (Mitchell, 2004)</p> <p>until 1989: some decrease in near-natural and secondary forest, especially along the edges of the forest glades and along the northern and eastern edge of the forest; afterwards: the trend reverses (bushland decreases in favour of secondary forest, hardly any agricultural land use can be found in the glades anymore) (Lung & Schaab, 2004)</p> <p>lowest logging levels were found in the northern Kakamega National and Nature Reserve, (central Ikuywa and Yala) (Bleher et al., 2005)</p>
Cut trees	9.1 per ha (Bleher et al., 2005)
Paths	0 per ha (Bleher et al., 2005)
Humidity	59.0 % (Althof, 2005)
Soil classification	Plinthic Lixisols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 4.9; C/N ratio: 10; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 120; $[\text{Ca}^{++}]$: 0; $[\text{Mg}^{++}]$: 11.3 (Musila et al., 2005)
Plant community	<i>Deinbollia kilimandscharica</i> – <i>Markhamia lutea</i> (Althof, 2005)
Succession stage	middle-aged secondary (Althof, 2005)
No. of plant species	103 (Evenness via Shannon-Wiener: 0.796) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	88.24 % (100 m buffer); 64.66 % (500 m buffer); 68.16 % (1,000 m buffer); 59.89 % (2,000 m buffer) (G. Schaab, pers. comm.)
Observed species	<i>Heinsenia diervilleoides</i> ;

Salazar circuit

Table 4: Characterization of the Salazar circuit study sites

Location	northern study site inside Kakamega Forest (Fig. 5)
Size	8,245 ha (Lung & Schaab, 2004)
Management regime	Kenya Wildlife Service (KWS)
Protection status	Nature Reserve
Disturbance history	<p>1913/16 map: shows the well-being of the forest at that time; 1977/78: Indiscriminately logging by Elgeyo Sawmill (Mitchell, 2004)</p> <p>until 1989: some decrease in near-natural and secondary forest, especially along the edges of the forest glades and along the northern and eastern edge of the forest; afterwards: the trend reverses (bush land decrease in favour of secondary forest, hardly any agricultural land use can be found in the glades anymore) (Lung & Schaab, 2004)</p> <p>Salazar II (as well as Yala) showed lowest disturbance levels per hectare (Bleher et al., 2005)</p> <p>lowest logging levels were found in the northern Kakamega National and Nature Reserve, (central Ikuywa and Yala) (Bleher et al., 2005)</p>
Cut trees	5/2 per ha (Salazar I/Salazar II) (Bleher et al., 2005)
Paths	2/1 per ha (Salazar I/Salazar II) (Bleher et al., 2005)
Humidity	68.6 % (Althof, 2005)
Soil classification	Haplic Ferrasols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 6.5; C/N ratio: 9; exchangeable bases in $\text{mmol} \cdot \text{kg}^{-1}$: CEC: 200; $[\text{Ca}^{++}]$: 340; $[\text{Mg}^{++}]$: 19.3 (Musila et al., 2005)
Plant community	<i>Deinbollia kilimandscharica</i> – <i>Markhamia lutea</i> (Althof, 2005)
Succession stage	middle-aged secondary (Althof, 2005)
No. of plant species	144 (Evenness via Shannon-Wiener: 0.703) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	96.88/94.28 % (100 m buffer in Salazar I/Salazar II); 84.43/94 % (500 m buffer in Salazar I/Salazar II); 75.34/92.03 % (1,000 m buffer in Salazar I/Salazar II); 75.57/82.87 % (2,000 m buffer in Salazar I/Salazar II) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> (Salazar); <i>Acanthus eminens</i> (Salazar I & II); <i>Heinsenias diervilleoides</i> (Salazar I)

Isecheno circuit

Table 5: Characterization of the Isecheno circuit study sites

Location	southern study site inside Kakamega Forest (Fig. 5)
Size	8,245 ha (Lung & Schaab, 2004)
Management regime	Forest Department (FD)
Protection status	Nature Reserve
Disturbance history	<p>northern study site: one of a few parts of the Kakamega Forest with just a few logging;</p> <p>southern study site: around 1931: logging in order to supply the gold mines with fuel and pit props; 1938: Mitchell Cotts & Co. Sawmill was operating a sawmill at the eastern end of the Isecheno Glade; 1972/73 until 1987: loss of large forest areas (Mitchell 2004)</p> <p>until the late 1980s: especially the southern parts of Kakamega were exploited (Bennun & Njoroge, 1999; Mitchell, 2004)</p> <p>cattle tracks appear to be a problem mostly at Isecheno (Bleher et al., 2005)</p>
Cut trees	9/12.5 per ha (northern/southern study site) (Bleher et al., 2005)
Paths	18.8 per ha (Bleher et al., 2005)
Humidity	79.4 % (Althof, 2005)
Soil classification	Eutric Cambisols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.9; C/N ratio: 5; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 230; $[\text{Ca}^{++}]$: 389; $[\text{Mg}^{++}]$: 51.9 (Musila et al., 2005)
Plant community	<i>Celtis mildbraedii</i> – <i>Craibia brownii</i> (Althof, 2005)
Succession stage	middle-aged secondary (Althof, 2005)
No. of plant species	163 (Evenness via Shannon-Wiener: 0.79) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	85.71/68.57 % (100 m buffer northern/southern study site); 81.86/69.01 % (500 m buffer northern/southern study site); 76.74/55.62 % (1,000 m buffer northern/southern study site); 67.32/45.5 % (2,000 m buffer northern/southern study site) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> (southern study site); <i>Acanthus eminens</i> (northern study site); <i>Heinsenias diervilleoides</i> (southern study site); <i>Dracaena fragrans</i> (southern study site)

4.2.2 Forest fragments study sites

Malava Forest

Table 6: Characterization of the Malava forest fragment

Location	northern forest fragment (Fig. 5)
Size	113 ha (Lung & Schaab, 2004)
Management regime	Forest Department (FD)
Protection status	Forest Reserve
Disturbance history	1910: definitely isolated from other forests, probably happened much earlier; 1940: FD records show start of intense logging (Mitchell 2004) 1980: decrease in near-natural forest and secondary forest the 1980s: forest plantations and bushed areas observed 2002: forest plantations disappeared in the most northern part and bushed area is used for agriculture again today: two fragments (Lung & Schaab, 2004)
Cut trees	9.2 per ha (Bleher et al., 2005)
Paths	8.8 per ha (Bleher et al., 2005)
Humidity	67.2 % (Althof, 2005)
Soil classification	Haplic Ferrasols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.8; C/N ratio: 7; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 230; $[\text{Ca}^{++}]$: 329; $[\text{Mg}^{++}]$: 28.5 (Musila et al., 2005)
Plant community	disturbed <i>Deinbollia kilimandscharica</i> – <i>Markhamia lutea</i> (Althof, 2005)
Succession stage	logged + planted forest (Althof, 2005)
No. of plant species	115 (Evenness via Shannon-Wiener: 0.749) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	79.41 % (100 m buffer); 32.99 % (500 m buffer); 20.54 % (1,000 m buffer); 15.15 % (2,000 m buffer) (G. Schaab, pers. comm.).
Observed species	<i>Heinsenia diervilleoides</i> [Rubiaceae]



Fig. 6: Aerial image of Malava Forest



Fig. 7: Aerial image of Kisere Forest (pictures from R. Steinbrecher 2001)

Kisere Forest

Table 7: Characterization of the Kisere forest fragment

Location	northern forest fragment (Fig. 5)
Size	420 ha (Lung & Schaab, 2004)
Management regime	Kenya Wildlife Service (KWS)
Protection status	Nature Reserve
Disturbance history	<p>20th century: never connected to Kakamega Forest by anything more substantial than probable connections along the Isiukhu and Nandamaywa Rivers (Tsingalia, 1988)</p> <p>1913/16 map: the same size as today (Mitchell 2004)</p> <p>1972-2001: wedge of secondary forest separating the near-natural forest into a northern and a southern part is generally closing again, secondary forest along the southern edge decreases slightly (Lung & Schaab, 2004)</p> <p>lowest logging levels were found in the northern Kakamega National and Nature Reserve, (central Ikuywa and Yala) (Bleher et al., 2005)</p>
Cut trees	10.4 per ha (Bleher et al., 2005)
Paths	2.3 per ha (Bleher et al., 2005)
Humidity	44.7 % (Althof, 2005)
Soil classification	Rhodic Ferrasols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.6; C/N ratio: 10; exchangeable bases in mmol _c •kg ⁻¹ : CEC: 150; [Ca ⁺⁺]: 126; [Mg ⁺⁺]: 24.7 (Musila et al., 2005)
Plant community	<i>Deinbollia kilimandscharica</i> – <i>Markhamia lutea</i> (Althof, 2005)
Succession stage	near-primary (Althof, 2005)
No. of plant species	138 (Evenness via Shannon-Wiener: 0.778) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	97.06/97.06 % (100 m buffer northern/southern study site); 69.47/70.20 % (500 m buffer northern/southern study site); 58.99/45.17 % (1,000 m buffer northern/southern study site); 29.81/32.87 % (2,000 m buffer northern/southern study site) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> (southern study site); <i>Acanthus eminens</i> (northern study site); <i>Heinsenya diervilleoides</i> (southern study site); <i>Dracaena fragrans</i>

Ikuywa Forest

Table 8: Characterization of the Ikuywa Forest fragment

Location	southern forest fragment (Fig. 5)
Size	1,370 ha (Lung & Schaab, 2004)
Management regime	Forest Department (FD)
Protection status	Forest Reserve
Disturbance history	<p>1913/16 map: shows the same eastern forest border; 1959 map: shows that a patch south and west of Ikuywa was connected to the Kakamega Forest; before the late 1950's: Ikuywa was not logged (Mitchell 2004)</p> <p>1972-2001: small changes in the north, 2001: a stronger share of bushes in the forest along the southern edge of the forest (Lung & Schaab, 2004)</p> <p>1979: the narrow connection between the Yala and Ikuywa forests was all but lost (Brooks et al., 1999)</p> <p>lowest logging levels were found in central Ikuywa, (the northern Kakamega National and Nature Reserve and Yala) (Bleher et al., 2005)</p>
Cut trees	3.8 per ha (Bleher et al., 2005)
Paths	10.8 per ha (Bleher et al., 2005)
Humidity	57.8 % (Althof, 2005)
Soil classification	Haplic Phaeozems (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.7; C/N ratio: 8; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 200; $[\text{Ca}^{++}]$: 255; $[\text{Mg}^{++}]$: 32.2 (Musila et al., 2005)
Plant community	<i>Celtis mildbraedii</i> – <i>Craibia brownii</i> (Althof, 2005)
Succession stage	middle-aged secondary (Althof, 2005)
No. of plant species	122 (Evenness via Shannon-Wiener: 0.718) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	97.14 % (100 m buffer); 66.05 % (500 m buffer); 50.74 % (1,000 m buffer); 33.14 % (2,000 m buffer) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> ; <i>Acanthus eminens</i> ; <i>Dracaena fragrans</i>

Yala Forest

Table 9: Characterization of the Yala Forest fragment

Location	southern forest fragment (Fig. 5)
Size	1,178 ha (Lung & Schaab, 2004)
Management regime	Forest Department (FD)
Protection status	Nature Reserve
Disturbance history	<p>in the 1950's: it became disconnected from the indigenous forest on the northern half of its boundary; Yala Nature Reserve has been never officially logged, but there was perennial pit-sawing of a few species (Mitchell 2004)</p> <p>1972-2001: in the southwest a permanent change in plantation forests and bushland, in the southeast a continuous loss of large areas of forest in favour of bushland (Lung & Schaab, 2004)</p> <p>Yala (as well as Salazar II) showed lowest disturbance levels per hectare (Bleher et al., 2005)</p> <p>lowest logging levels were found in Yala, (the northern Kakamega National and Nature Reserve and central Ikuywa) (Bleher et al., 2005)</p>
Cut trees	2.8 per ha (Bleher et al., 2005)
Paths	0 per ha (Bleher et al., 2005)
Humidity	83.8 % (Althof, 2005)
Soil classification	Chromic Cambisols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 5.9; C/N ratio: 6; exchangeable bases in $\text{mmol}_c \cdot \text{kg}^{-1}$: CEC: 170; $[\text{Ca}^{++}]$: 196; $[\text{Mg}^{++}]$: 13.3 (Musila et al., 2005)
Plant community	<i>Celtis mildbraedii</i> – <i>Craibia brownii</i> (Althof, 2005)
Succession stage	old secondary (Althof, 2005)
No. of plant species	120 (Evenness via Shannon-Wiener: 0.784) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	90.91 % (100 m buffer); 78.57 % (500 m buffer); 61.13 % (1,000 m buffer); 53.58 % (2,000 m buffer) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> ; <i>Acanthus eminens</i> ; <i>Heinsenia diervilleoides</i> ; <i>Dracaena fragrans</i>

Kaimosi Forest

Table 10: Characterization of the Kaimosi Forest fragment

Location	southern forest fragment (Fig. 5)
Size	65 ha (Lung & Schaab, 2004)
Management regime	Forest Department (FD)
Protection status	Forest Reserve
Disturbance	1913/16 map: shows an unbroken forest of Kakamega and Kapwaren Forest (now: South Nandi Forest); between 1913 and 1959: gradually eroded; 1965: pit-sawing of local the locals (Mitchell 2004) 1972-2001: increase in bushland from the south, while forest area is spreading in the northeast 2001: the southern fragments mostly consist of bushland, in the northwest existing forest plantation disappeared (Lung & Schaab, 2004)
Cut trees	30 per ha (Bleher et al., 2005)
Paths	18.3 per ha (Bleher et al., 2005)
Humidity	67.2 % (own estimation)
Soil classification	Eutric Cambisols (Musila et al., 2005)
Chemical properties of soil (A-horizon)	pH-value: 4.5; C/N ratio: 10; exchangeable bases in $\text{mmol}\cdot\text{kg}^{-1}$: CEC: 100; $[\text{Ca}^{++}]$: 58; $[\text{Mg}^{++}]$: 6.4 (Musila et al., 2005)
Plant community	<i>Celtis mildbraedii</i> – <i>Craibia brownii</i> (Althof, 2005)
Succession stage	heavily logged and planted (Althof, 2005)
No. of plant species	93 (Evenness via Shannon-Wiener: 0.665) (Althof, 2005)
Forest in buffer zones in concentric circles around study site mid points	83.33 % (100 m buffer); 41.73 % (500 m buffer); 17.65 % (1,000 m buffer); 6.94 % (2,000 m buffer) (G. Schaab, pers. comm.)
Observed species	<i>Acanthopale pubescens</i> ;

5. Material and methods

“The primary technique of pollination ecology [...] is the same today as in Sprengel’s or Darwin’s days: consistent observation of what really happens in nature, in the original, natural habitat of the plant under investigation.”

(Faegri & van der Pijl, 1979)

5.1 Study plant species

This study was conducted on four plant species that were abundant enough to facilitate statistical analyses (*Acanthopale pubescens* [Acanthaceae], *Acanthus eminens* [Acanthaceae], *Heinsenia diervilleoides* [Rubiaceae] and *Dracaena fragrans* [Ruscaceae]).

The first field campaign June 2001 to December 2001 focused on the moist Afromontane forest understorey shrub *Acanthopale pubescens*. After this *Acanthus eminens* another moist Afromontane forest understorey Acanthaceae was observed in two campaigns: January 2002 to March 2002 and November 2002 to February 2003. The third plant species under examination was *Heinsenia diervilleoides*, a small tree generally found in Afromontane and Guineo-Congolian forests. *Heinsenia diervilleoides* individuals were observed from November 2002 to March 2003. The fourth campaign was conducted between July 2002 and April 2003 and focused on the common Guineo-Congolian forest shrub *Dracaena fragrans*.

In different studies, various study sites were taken into consideration, because of the fact that not every plant species examined was found blooming everywhere. Consequently, different observation plots were conducted inside particular study sites (Table 11).

Table 11: Study sites with flowering plant species (grey box) during field campaigns

	<i>Acanthopale pubescens</i> [Acanthaceae]	<i>Acanthus eminens</i> [Acanthaceae]	<i>Heinsenia diervilleoides</i> [Rubiaceae]	<i>Dracaena fragrans</i> [Ruscaceae]
Colobus trail				
Buyangu hill				
Salazar circuit		Salazar I & II	Salazar I	
Isecheno circuit	southern part	northern part	southern part	
Malava Forest				
Kisere Forest	northern part	southern part	southern part	
Ikuywa Forest				
Yala Forest				
Kaimosi Forest				

5.1.1 *Acanthopale pubescens* (Lindau ex Engl.) C.B. Clarke [Acanthaceae]

Acanthaceae is a large pantropical family of about 250 genera and 2,500 species with four centres of distribution: Africa, Indo-Malaya, Brazil and Central America northward into Mexico (Kokwaro, 1994).

Acanthopale pubescens itself is an erect, sometimes hairy, branched shrub with elliptic leaves gradually narrowed at its base and apex. In the upper half the leaf is winged (Agnew & Agnew, 1994). Inflorescences are lateral and terminal (Fig. 8A/C). *Acanthopale pubescens* generates white, hermaphroditic and radial symmetric flowers which are hairy on the inside; in addition they are spotted and have pink and purple stripes (Fig. 8C/D). Corollas are up to 3 cm long and variable in size (Fig. 8B) (Kraemer, 2002). The anthesis of a flower takes approximately three days (pers. obser.).

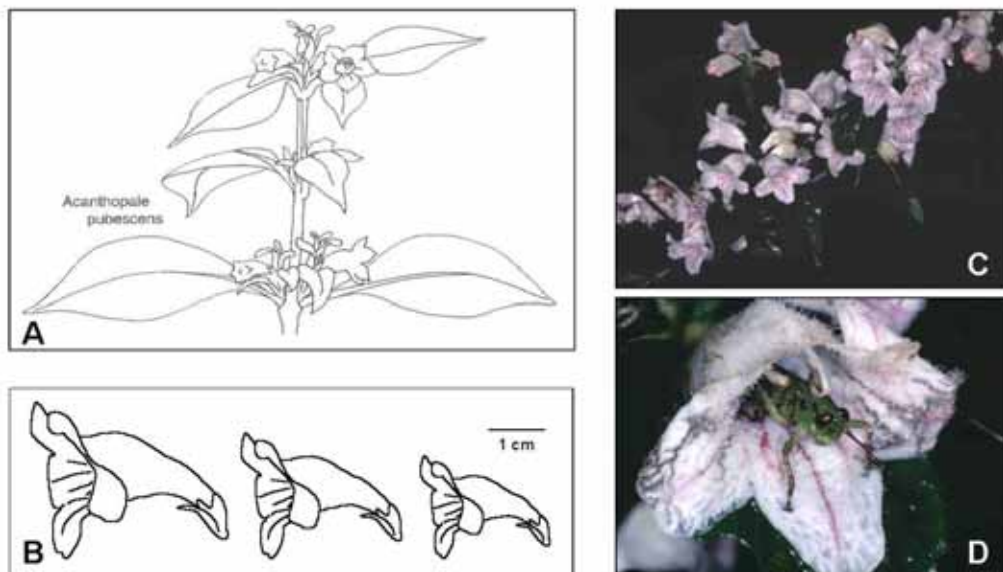


Fig. 8: (A) *Acanthopale pubescens* (Acanthaceae) (Agnew & Agnew, 1994), (B) flowers (simplified lateral view). Flowers are highly variable in size (Kraemer, 2002), (C) several inflorescences, (D) flower with visitor (picture from M. Kraemer 2001)

Acanthopale pubescens offers a plietesial flowering cycle, it produces just once or a few times a decade huge numbers of flowers (mass blooming); followed by a synchronised die off of the entire plant population (pers. obser.). This mass blooming is constricted to a period of about four weeks. Approximately four to six weeks after fertilization loculicidal spindle-shaped capsules (up to 13mm long; pers. obser.) begin to emerge. Its fruits contain a maximum of seeds due to their four ovules.

Acanthopale pubescens is distributed in moist Afromontane forests at an altitude of 1,655 to 2,790m (Agnew & Agnew, 1994) and can mainly be found along forest trails and in forest gaps. Here, it is regarded as a species of an early climax succession stage in more or less disturbed moist Afromontane forests (Althof, 2005).

5.1.2 *Acanthus eminens* (C.B. Clarke) [Acanthaceae]

Acanthus eminens is a woody herb or shrub that is approximately five meters high. The leaves are oblong, pinnatifid or lobate with spiny leaf margins. These spines are also present at the base of the petioles (Beentje, 1994). In dense, up to 35cm (Beentje, 1994) long terminal stachoids royal blue to purple zygomorphic and hermaphroditic flowers follow each other from the bottom upwards (Fig. 9A/D). The flowers are characterised

by four monothealous stamens with thick, bone-like filaments (Fig. 9B) (McDade & Moody, 1999). The four one-sided petals fuse into a sympetalous lobed corolla (Dietzsch, 2004). The anthesis of a flower is approximately three to four days (pers. obser.).

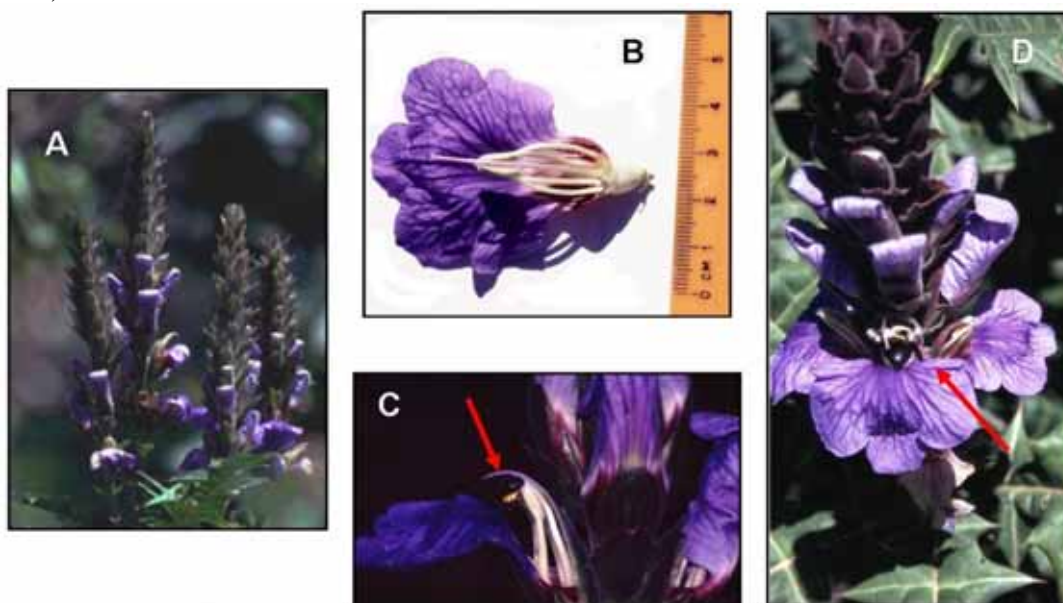


Fig. 9: (A) *A. eminens* with several inflorescences (picture from A. Dietzsch 2004), (B) flower of *A. eminens* (picture from K. Gebhardt 2004), (C) *A. eminens* with visitor (picture from A. Dietzsch 2004), (D) *A. eminens* with visitor

Approximately four to six weeks after fertilization (pers. obser.) loculicidal club-shaped capsules (to 18mm long, (Beentje, 1994)) begin to emerge with four potential seeds, two at each side of its woody septum.

Acanthus eminens is distributed in moist Afromontane forests at an altitude of 1,500 to 2,800m (Agnew & Agnew, 1994) and prefers moist and sunny sites. In addition, it is regarded as a species of a late climax succession stage in less disturbed Afromontane forests (Althof, 2005).

5.1.3 *Heinsenia diervilleoides* (K. Schum.) [Rubiaceae]

The Rubiaceae is a large pan tropical and subtropical family of about 500 genera and 6,000 species (Kokwaro, 1994).

Heinsenia diervilleoides is an evergreen, grey shrub or tree that grows to approximately 12m in height. The glabrous to puberulous, narrowly elliptic leaves often show reddish veins underneath. Furthermore, the base of the leaf is cuneate and the apex acuminate with a long acute tip (Beentje, 1994). Several-flowered inflorescences and later fruits are axillary or in forks (Fig. 10A). The hermaphroditic and radial symmetric flowers of *Heinsenia diervilleoides* are white with pink spots inside (Fig. 10B). Corollas are hairy and up to 20mm long (Beentje, 1994). The anthesis of a flower is approximately three to four days (pers. obser.).



Fig. 10: (A) *Heinsenia diervilleoides* K. Schum. (Rubiaceae) (Beentje, 1994),
(B) Several inflorescences

Approximately six to eight weeks after fertilization (pers. obser.) round, greenish-purple berries crowned with a persistent calyx begin to appear (Beentje, 1994). The up to 13mm in diameter sized fruits (Beentje, 1994) contain a maximum of two seeds due to their two ovules.

In general, *H. diervilleoides* can be found in Afromontane and Guineo-Congolian forests at an altitude of 200 to 2,300m (Beentje, 1994). Here, it is regarded as a species of a late climax succession stage in East African forests (Althof, 2005).

5.1.4 *Dracaena fragrans* (L.) Ker Gawl. [Ruscaceae]

Dracaena fragrans is an unbranched shrub or tree that reaches up to approximately 15m in height. In Kenya, however, it is just up to five metres high (Beentje, 1994). The glabrous leaves are narrowly elliptic. Furthermore, the base of the leaf is narrowed, but spreading at the amplexicaul extreme, and the apex is acute. Inflorescences are arranged in panicles of white hermaphroditic and radial symmetric flowers with exposed stamens and filaments out of the up to 18mm long corollas (Beentje, 1994) (Fig. 11A/B). The anthesis of a flower is approximately two to three days (pers. obser.).



Fig. 11: (A) several inflorescences, (B) Caleb Analo showing inflorescences of *D. fragrans*

Approximately six to eight weeks after fertilization (pers. obser.) round and sometimes lobed, fleshy and orange fruits are appearing (Beentje, 1994). The up to 18mm diameter sized berries (Beentje, 1994) contain a maximum of three seeds due to their three ovules.

Dracaena fragrans is mainly distributed in Guineo-Congolian forests at an altitude of 1,550 to 1,850m (Beentje, 1994). Here, it is regarded as a species of a late climax succession stage in Guineo-Congolian forests (Althof, 2005).

5.2 Visitation frequency

Visitation frequency is defined as number of visits per flower per time unit. The units in this study lasted one hour.

In general, all observations of visitor activities were conducted in randomly selected plots between 9 a.m. and 2 p.m. After finishing one hour of observation, a new plot was chosen.

In addition, detailed information concerning the visitor type and the visitor behaviour was recorded, e.g. whether the visitors collect pollen and/or nectar, and how long the duration of their stay was.

5.3 Primary pollination success

Primary pollination success, as defined in this study, is the number of pollen grains per stigma.

Firstly, the collected stigmas (see chapter 6 for collecting period and number of collected stigmas), which were dissected from the flowers of the different observed plant species were preserved in 98 % ethanol. Then, they were stained for ten minutes in a aniline blue combined stain (1g aniline blue, 1g calcofluor (brightener), 3.5g tribasic potassium phosphate (K_3PO_4) (Kearns & Inouye, 1993)) to determine the pollen grains deposited on the stigmas. Each component was separately dissolved in distilled water. In addition, it was mixed with Aqua dest. and finally topped up to the volume of one litre. After ten minutes staining, the slide was covered with a cover slip.

Pollen grains were counted under the ultraviolet light of an Olympus SZH microscope; the pictures were taken by Olympus microscope digital camera system DP50 (Fig. 15; Fig. 26; Fig. 38; Fig. 44), while the scales calculations and their burning into digital images were assisted by analySIS[®] 3.1 software.

The number of deposited pollen of all plant species were checked and counted inside the entire receptive region on the stigmas. One exception was *H. diervilleoides*, because here the counts were restricted to a defined apical region – from the region upwards where the stigma splits - due to the great number of pollen deposited.

5.4 Self-fertilisation field test

To determine whether the observed plant species is potentially capable of self-fertilisation (autogamy), marked plant individuals were manipulated by applying their own pollen onto the receptive stigmas. After that, the flowers were covered with net bags to prevent animals from visiting them.

Thus, at least three individual flowers were tested (*Acanthopale pubescens* (n=9), *Acanthus eminens* (n=10), *Heinsenia diervilleoides* (n=3) and *Dracaena fragrans* (n=9)).

5.5 Fruit set and seed set

The terms “pollination efficiency” and “pollination success” have been used in different ways by different researchers (Kearns & Inouye, 1993). In this study seed and fruit set are defined as indicators for pollination success.

After collecting the fruits, its fruit set was calculated by dividing harvested fruits by potential fruits (counted flowers). After that, the seed set was determined by dividing counted seeds per fruit by potential ovules of the specific plant species:

$$\text{fruit set} = \frac{\text{harvested fruits}}{\text{potential fruits}} \quad ; \quad \text{seed set} = \frac{\text{counted seeds}}{\text{potential ovules}} .$$

5.6 Considered biotic factors

Apart from the “number of observed flowers”, the following biotic factors were considered in the statistics of each campaign on different levels of pollination (frequency of flower visits, primary pollination success, fruit and seed set).

Number of observed flowers

All intraspecific flowers were counted in each observation plot related to every observation unit, verifying the potential influence of intraspecific flower quantity on the visitation frequency. *Acanthopale pubescens*, *Acanthus eminens* and *Heinsenia diervilleoides* flowers were counted.

Abundance of the plant species

Plant individuals of *Acanthopale pubescens* and *Acanthus eminens* were conducted in transects of 100m in length and about 4m in width inside all study sites (M. Kraemer, pers. comm.). In contrast, *H. diervilleoides* and *D. fragrans* plant counts were carried out in 10x10m relevés inside every forest fragment (Althof, 2005), but in each case the final abundance of the plant species resulted in an average value calculation on study site level.

These data were used in order to test potential plant abundance effects.

Plant species richness

Within the framework of vegetation surveys by Althof (2005) species lists of trees, shrubs and climbers of all forest fragments were generated. These varying number of plant species inside all forest fragments were used for finding potential impacts of the richness of plant species on different levels of pollination.

Shannon-Wiener index of species diversity (H')

Apart from the number of plant species, the α -diversity calculations with the aid of Shannon-Wiener function and Shannon’s evenness (E_H) were available (Althof, 2005) to analyse possible correlations between plant species diversity and collected data.

Here Shannon’s evenness (E_H) was considered and calculated by dividing H' by H'_{\max} that assumes a value between 0 and 1 with 1 indicating the complete evenness.

Fragmentation (direct factor)

The forest remnants were categorised into main forest fragment study sites (subsequently called: main forest) and surrounding forest fragment (subsequently called: forest fragment) study sites to test all data on potential forest fragmentation effects.

Succession stages

Categorisations of the Kakamega Forest fragments in different succession stages (near-primary, old secondary, middle-aged secondary, young secondary and heavily logged and planted) were also available (Althof, 2005) for testing the influence of succession on the different levels of pollination .

Percentage of forest in a defined buffer zone (=circumferences)

On the basis of a LANDSAT 7 (ETM+) satellite image (band combination 5/4/3, contrast enhanced) of Kakamega Forest of February 5, 2001, land cover was interpreted by digital image processing with ArcGIS® 8.x (Lung & Schaab, 2004) in concentric circles around study site mid points by Schaab. Inside the 100m, 500m, 1,000m and 2,000m buffers the percentage of forest cover was determined in order to analyse potential edge effects.

Cut trees per hectare

In an assessment of the threat status and the management effectiveness in the Kakamega Forest, disturbance surveys were carried out at 22 forest sites (Bleher et al., 2005). Here trail transects were run at least 1,000m in length recording disturbance parameters, like logged trees, in a belt of 10m on each side of the transects. The total number of logged trees per hectare was integrated in this thesis statistics to analyse the effect of logging disturbance.

5.7 Considered abiotic factors

Apart from “temperature and cloudiness” and “pH-value, C/N ratio, Cation Exchange Capacity (CEC), [Ca⁺⁺], [Mg⁺⁺]” all of the following abiotic factors were considered in the statistics concerning the different levels of pollination (frequency of flower visits, primary pollination success, fruit and seed set) for all examined plant species.

Management type

The Kakamega Forest and its peripheral fragments are managed under the authority of both the Forest Department (FD) and the Kenya Wildlife Service (KWS) on behalf of the state. This allowed analysing a potential influence of different management regimes (Fig. 4).

Protection status

Kakamega Forest and its five surrounding fragments are partly a Forest Reserve, partly a Nature Reserve and partly a National Reserve (Fig. 4). This study distinguishes between sites with high protection priority, i.e. National or Nature Reserves and sites with low protection priority, i.e. Forest Reserves. Consequently, all data was analysed concerning a potential forest protection impact.

Size of forest fragments

On the basis of a LANDSAT 7 (ETM+) satellite image (band combination 5/4/3, contrast enhanced) of the Kakamega Forest February 5, 2001, the size of all forest areas were visually interpreted Schaab (2004). This interpretation allowed testing the fragment size as an interfering factor.

North-south gradient

Representing a potential microclimatic factor of the Kakamega Forest region, a north-south gradient was included in this study. Here, the forest fragments were numbered consecutively southwards.

Paths per hectare

As an indicator of human disturbance, paths per hectare in each forest fragment were integrated in this study. Here, trail transect walks of at least 1,000 m in length, were conducted recording all crossing paths (Bleher et al., 2005).

Humidity

Humidity was measured by two types of Gemini[®] data loggers: Tinytag Plus (air temperature and humidity) and Tinytalk (humidity), while data was recorded every hour inside all study sites with exception of the Kaimosi forest fragment (Althof, 2005). Due to the correlation between measured humidity and environment conditions, the average humidity of the similar structured Malava forest fragment was assumed. (*“The more open a canopy was and the more sunlight could reach the ground, the lower was the measured humidity”* (Althof, 2005)).

Temperature and cloudiness

Observations of visitors' activities were conducted in randomly selected plots between 9 a.m. and 2 p.m.. Thus, the temperature was measured every hour with a mercury thermometer, while the cloudiness was estimated in eighths. The average temperature and average cloudiness of all units in each study site was used for analysing potential relations between visitation frequency, temperature and cloudiness, respectively.

pH-value, C/N ratio, Cation Exchange Capacity (CEC), [Ca⁺⁺], [Mg⁺⁺]

In all study sites one pit was excavated to up about 2 m and described according to standard procedures of the Food and Agriculture Organization (FAO) Guidelines for soil profile descriptions (FAO, 1977). The soil horizons were identified and analysed by W. Musila with the help of the Kenya Soil Survey (Musila et al., 2005). In this study A-horizon values were considered. Regarding visitation frequency and primary pollination success, the pH-value and the C/N ratio were tested. With reference to fruit and seed set all available soil parameters were considered.

5.8 Statistics

In general, Cane (2001) annotate a lack of universal and satisfying strategies for meaningful, insightful, and flexible statistical analyses in fragmentation studies.

In this study the received data was listed with Microsoft[®] Excel 2000 and analysed with SPSS[®] 12.0 for Windows[®].

All results of different levels of pollination (frequency of flower visits, primary pollination success, fruit and seed set), separated into plant species, were tested on the assumption of normal distribution by the Kolmogorov-Smirnov goodness-of-fit test on

study site level. Although not all data on study site level showed a standard normal distribution, they were treated so here in parametric methods, due to the biological presumptions of these ecological processes (Underwood, 1997).

Varieties between the grouped main forest and forest fragment study sites and the *D. fragrans* covering experiment were tested by one-way analysis of variance (ANOVA).

In a Pearson correlation analysis the potential influence of the measured biotic and abiotic factors on the different levels of pollination were tested (see Appendices). Factors showing a significant correlation ($\alpha \leq 0.05$) were tested for multi-collinearity by a linear regressions analysis (Backhaus et al., 2003). In the case of $R^2 \geq 0.7$ factors were considered redundant. Finally, all remaining factors were tested in a backward multiple regressions (variables were successively removed from the model, if the significance level of the parameter estimate was higher than $p = 0.10$). Significant correlations ($p \leq 0.05$) were indicated with one star (*) and highly significant correlations ($p \leq 0.01$) respectively with two stars (**).

In the interest of a better descriptiveness, the data was presented in box plots (a box around 50% of the data and lines from the minimum to the first quartile and from the maximum to the third quartile; black bar indicates 50% percentile = median). Exceptions were diagrams concerning seed sets; due to their narrow margin of data scale error bars were used.

6. Results

The results are listed separately for each plant species (*Acanthopale pubescens* [Acanthaceae], *Acanthus eminens* [Acanthaceae], *Heinsenia diervilleoides* [Rubiaceae] and *Dracaena fragrans* [Ruscaceae]). Furthermore, they are subdivided into the different levels of pollination (frequency of flower visits, primary pollination success, fruit and seed set).

6.1 *Acanthopale pubescens* [Acanthaceae]

6.1.3 Visitation frequency

During the 254 hours of observation between the June 28 and the August 9, 2001, it became evident that the mainly white flowers of *A. pubescens* were attractive for a variety of insects. In total, 656 visitors were counted on 30,722 observed flowers during 254 observation units. This study was conducted in three main forest (Colobus trail, Salazar and Isecheno) and four forest fragment (Kisere, Ikuywa, Yala and Kaimosi) sites.

The most probable pollinator of *A. pubescens* appeared to be honey bees (*Apis mellifera*) due to their size and the permanent contact with stigmas inside the flowers. Therefore, smaller bees like halictids and different sized butterflies will not be considered in the following statistics.

Approximately 80% (542) of the flower visitors were honey bees. Even so, the share of honey bee visits differed between 42% (33 of 79) at Salazar to 100% (40 of 40) in Isecheno. In 23.6% (60) of all observation units no honey bee visits at all were detected (Table 12).

Table 12: Observation units without honey bee visits (*A. pubescens*)

Study site	% of units without honey bee visit	Number of units (units without honey bee visit/ all units)
Colobus trail	19.6	9/46
Salazar	26.5	9/34
Isecheno	37	10/27
Kisere	9.3	5/54
Ikuywa	23.5	8/34
Yala	40.5	15/37
Kaimosi	18.2	4/22

The mean visitation frequency of honey bee on *A. pubescens* flowers amounted to 0.16 visits/flower/hour (SD: 0.20).

Among all study sites, the northern forest fragment Kisere showed the highest mean honey bee visitation frequency of 0.26 visits/flower/hour (SD: 0.26). The lowest mean honey bee visitation frequency of 0.08 visits/flower/hour (SD: 0.11) was found inside the observed *A. pubescens* population of the southern forest fragment, Yala. However, with reference to the mean visitation frequency between the different study sites, no significant differences were apparent (Table 13; Fig. 12A).

Table 13: Mean visitation frequencies (*A. pubescens*)

Study site	Visitation frequency	Standard deviation (SD)
Colobus trail	0.19	0.26
Salazar	0.08	0.09
Isecheno	0.11	0.17
Kisere	0.26	0.26
Ikuywa	0.12	0.12
Yala	0.08	0.11
Kaimosi	0.18	0.17

When comparing main forest (0.14 visits/flower/hour/ SD: 0.20) with forest fragment (0.17 visits/flower/hour/ SD: 0.20), a slightly ($p=0.177$) higher visitation frequency in main forest plots is evident (Fig. 12B).

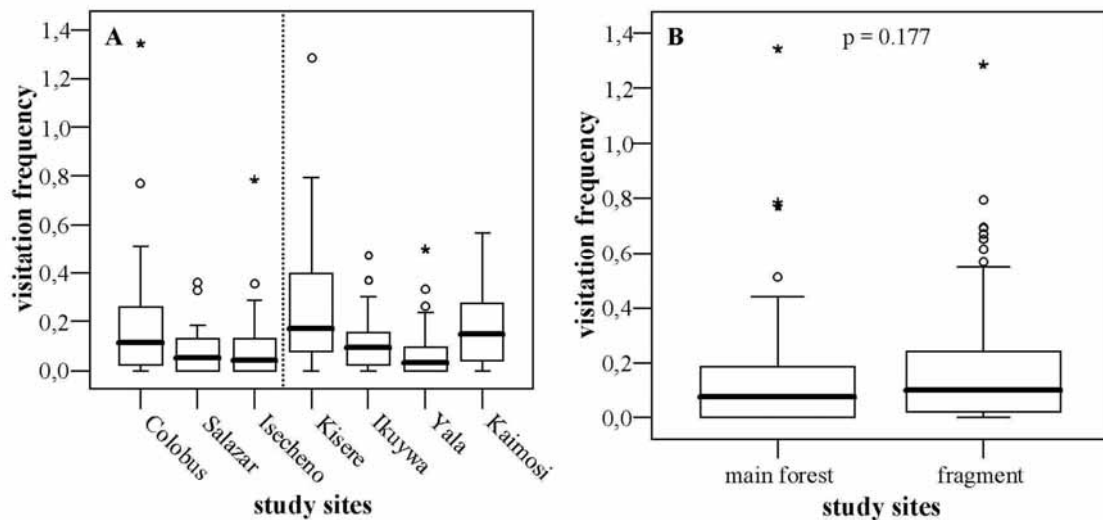


Fig. 12: Visitation frequencies on *A. pubescens* by honey bees (*Apis mellifera*) (box plots):
(A) in three main forest (left of the dashed line) and four forest fragment study sites (right of the dashed line) arranged from north to south,
(B) grouped in main forest (3) and forest fragment (4) study sites
[(B) tested for differences by one-way ANOVA]

Influences of relevant biotic and abiotic factors on the mean honey bee visitation frequency were analysed by a backward multiple regression. The final model ($R^2=0.125$) indicated that the number of observed flowers ($p=0.022^*$), the percentage of forest surrounding the observation areas in a buffer of 2,000m ($p=0.002^{**}$) and a north-south gradient ($p<0.001^{**}$) potentially influenced the honey bee visitation frequency (Table 14). All three factors showed an inverse proportion regarding honey bee visitation frequencies.

Honey bee visitation frequencies rose with a lower number of observed flowers, with a lower percentage of forest surrounding the observation areas in a buffer of 2,000m (range: about 10% – 80%) and from south to north (Table 14; Fig. 13).

Table 14: Final model coefficients of a backward multiple regression (started with n=7 factors; Appendix 11)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.377	.039		9.662	.125	< .001**
Number of observed flowers	.000	.000	-.143	-2.305		.022*
% of forest in a 2,000m buffer	-.002	.001	-.198	-3.199		.002**
North-south gradient	-.022	.006	-.225	-3.794		< .001**

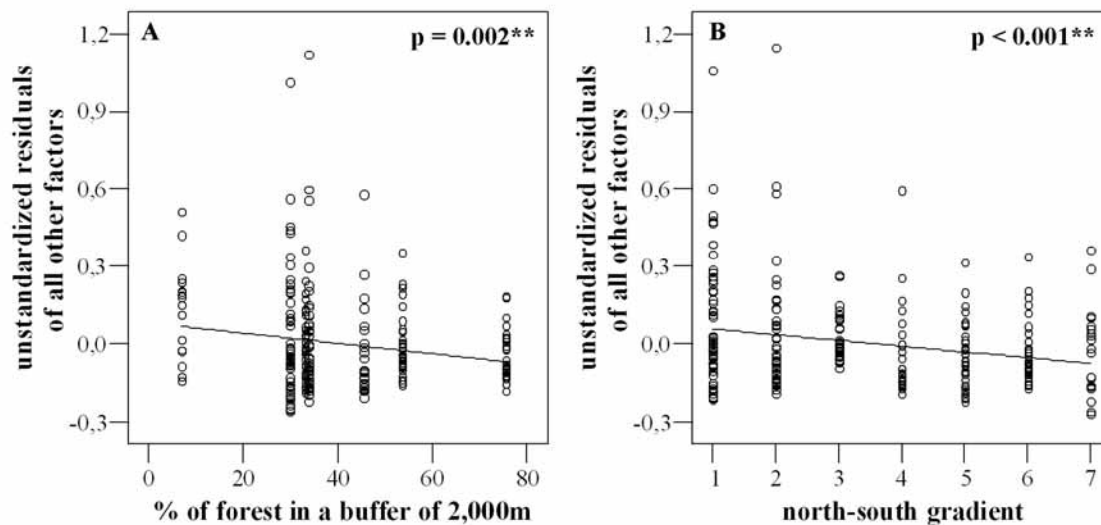


Fig. 13: Regression scatter plots *A. pubescens* (dependent variable= visitation frequencies): (A) percentage of forest surrounding the observation areas in a buffer of 2,000m to unstandardized residuals of the factors north-south gradient and number of observed flowers, (B) north-south gradient (1=northernmost; 7=southernmost) to unstandardized residuals of the factors percentage of forest surrounding the observation areas in a buffer of 2,000m and number of observed flowers

A multiple regression model ($R^2=0.924$) on study site level confirmed the potential impact of the factors north-south gradient ($p=0.008^{**}$) and the percentage of forest surrounding the observation areas in a buffer of 2,000m ($p=0.004^{**}$) (Table 15; Fig.14).

Table 15: Coefficients of a multiple regression (n=2 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.340	.029		11.603	.924	< .001**
% of forest in a 2,000m buffer	-.003	.000	-.859	-6.024		.004**
North-south gradient	-.022	.004	-.707	-4.956		.008**

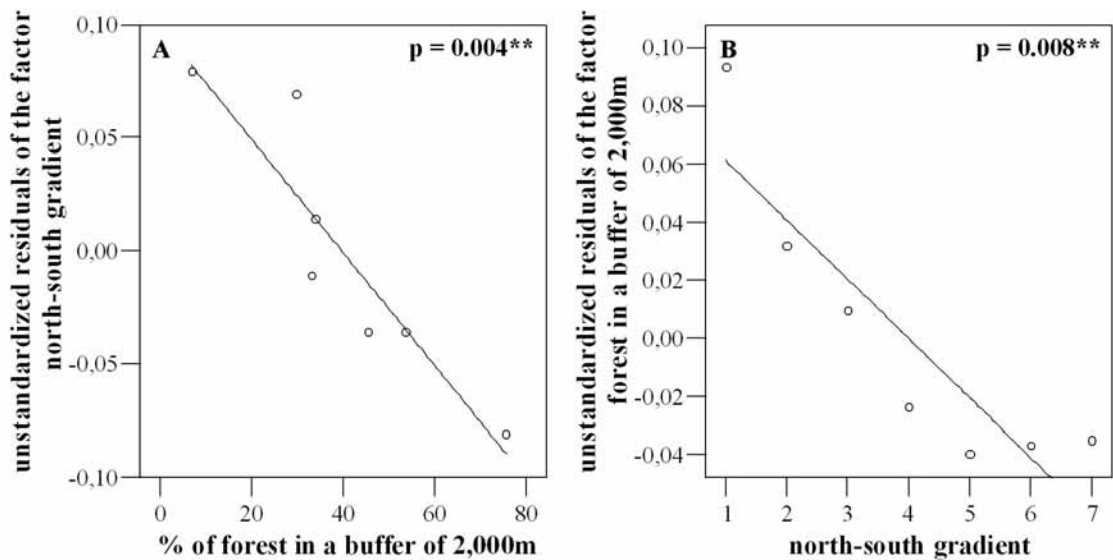


Fig. 14: Regression scatter plots *A. pubescens* study sites

(depend. variable= visitation frequencies):

(A) percentage of forest surrounding the observation areas in a buffer of 2,000m to unstandardized residuals of the factor north-south gradient,

(B) north-south gradient (1=northernmost; 7=southernmost) to unstandardized residuals of the factor percentage of forest surrounding the observation areas in a buffer of 2,000m

6.1.2 Primary pollination success

Inside the seven *A. pubescens* study sites 143 stigmas were collected, distributed in Colobus trail (13); Salazar (27); Isecheno (27); Kisere (27); Ikuywa (24); Yala (14) and Kaimosi (11). After that, the pollen grains were counted under a fluorescence microscope (Fig. 15).

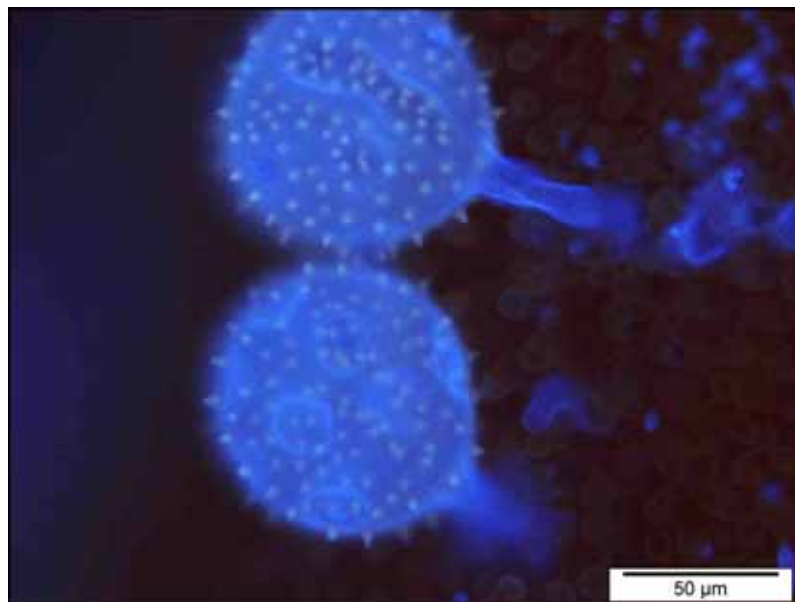


Fig. 15: *Acanthopale pubescens* [Acanthaceae] pollen connected with the stigma by pollen tubes

65% (93 of 143) of all the investigated stigmas were loaded with at least one pollen. The highest percentage of loaded stigmas was found in Kaimosi with 90.9% (10 of 11) and the lowest was found in Ikuywa with only 25% (6 of 24) (Table 16).

Table 16: Percentage of stigmas loaded with pollen (*A. pubescens*)

Study site	% of stigmas loaded with pollen	Number of stigmas (stigmas loaded with pollen/ all stigmas)
Colobus trail	84.6	11/13
Salazar	81.5	22/27
Isecheno	63	17/27
Kisere	74.1	20/27
Ikuywa	25	6/24
Yala	50	7/14
Kaimosi	90.9	10/11

All 143 stigmas of *A. pubescens* collected showed the mean pollen number per stigma of 5.5 (SD: 7.52). Regarding the different study sites, no significant differences were apparent (Fig. 16A; Table 17). The highest number of deposited pollen (37) on stigmas was found at the Colobus trail.

Table 17: Mean pollen number per stigma (*A. pubescens*)

Study site	Pollen number per stigmas	SD
Colobus trail	15.23	12.98
Salazar	4.89	5.56
Isecheno	4.11	5.94
Kisere	7.00	6.99
Ikuywa	1.04	2.31
Yala	3.21	4.82
Kaimosi	7.27	8.13

When comparing the counted pollen on stigmas in main forest (6.58/SD: 8.67) with forest fragment (4.46/SD: 6.24), a non significant ($p=0.093$) higher mean number of pollen on stigmas was counted inside the main forest (Fig. 16B).

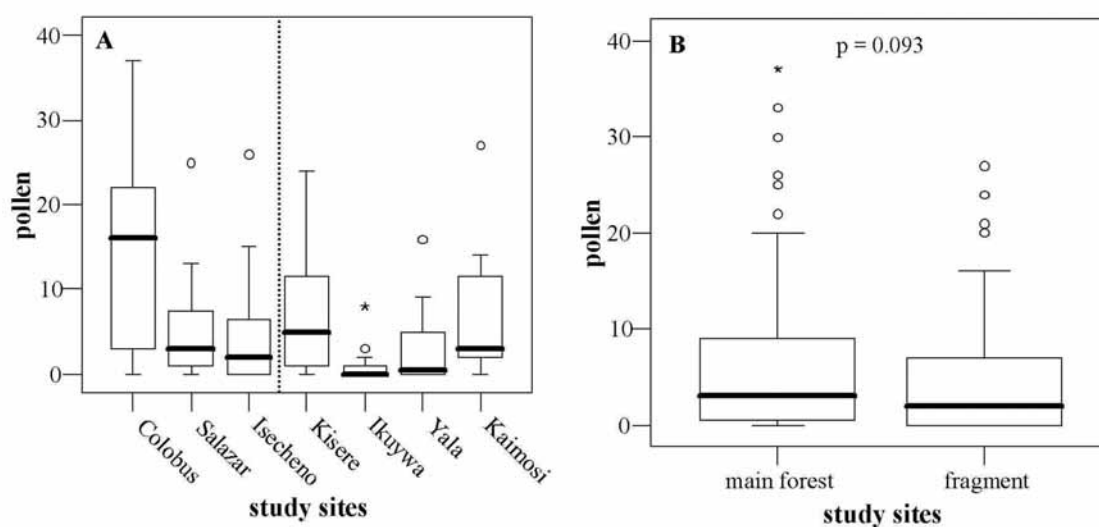


Fig. 16: Counted pollen on stigmas of *A. pubescens* (box plots):
 (A) in three main forest (left of the dashed line) and four forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (3) and forest fragment (4) study sites
 [(B) tested for differences by one-way ANOVA]

The percentage of stigmas loaded with pollen was also higher in main forest study sites (Table 18).

Table 18: Percentage of stigmas loaded with pollen (*A. pubescens*)

Study site	% of stigmas loaded with pollen	Number of stigmas (stigmas loaded with pollen/ all stigmas)
Main forest	74.6	50/67
Forest fragment	56.6	43/76

The potential influence of obtained abiotic and biotic factors on the number of pollen on *A. pubescens* stigmas were analysed by a backward multiple regression. Here, the final model indicated ($R^2=0.118$) with high significance that the protection status (nature or forest reserve) ($p=0.005^{**}$) and the C/N ratio of the soil ($p<0.001^{**}$) might have an effect on the number of pollen deposited on the stigmas (Table 19).

A higher amount of pollen on the stigmas was found in nature reserves as compared to forest reserve study sites. In addition, more pollen on stigmas was found in forests with a higher C/N ration in the soil (range: 5 – 10).

Table 19: Final model coefficients of a backward multiple regression (started with n=3 factors; Appendix 13)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	1.123	2.932		.383	.118	.702
C/N ratio	1.142	.313	.292	3.647		< .001**
Protection status	-3.989	1.399	-.229	-2.852		.005**

Self-pollination experiments showed an ability for autogamy as 33% (n=9) of the tested plant individuals produced at least one seed. But, generally, these seeds looked poorer and smaller than regular pollinated ones.

6.1.3 Fruit set

Between August 24 and December 21, 2001, 9641 *Acanthopale pubescens* fruits were picked. All in all, the fruit set of 140 marked individuals were observed, distributed in Colobus trail (13); Salazar (18); Isecheno (25); Kisere (14); Ikuywa (21); Yala (20) and Kaimosi (29).

5% (7) of the observed individuals developed no fruits. The same number of individuals (5%/7) produced the maximum potential fruit number (fruit set: 1.0). During this campaign, *A. pubescens* showed a mean fruit set of 0.59 (SD: 0.29).

A general tendency of a higher fruit set inside the main forest compared to forest fragments became apparent (Table 20; Fig. 17A).

Table 20: Mean fruit set (*A. pubescens*)

Study site	Fruit set	(SD)
Colobus trail	0.68	0.21
Salazar	0.72	0.27
Isecheno	0.72	0.27
Kisere	0.59	0.27
Ikuywa	0.42	0.32
Yala	0.48	0.31
Kaimosi	0.54	0.22

A comparison of the grouped study sites in main forest (0.71/SD: 0.25) and forest fragment sites (0.51/SD: 0.28) confirmed this first assumption and documented a highly significant ($p < 0.001^{**}$) lesser fruit set of *A. pubescens* inside the forest fragment plots (Fig. 17B).

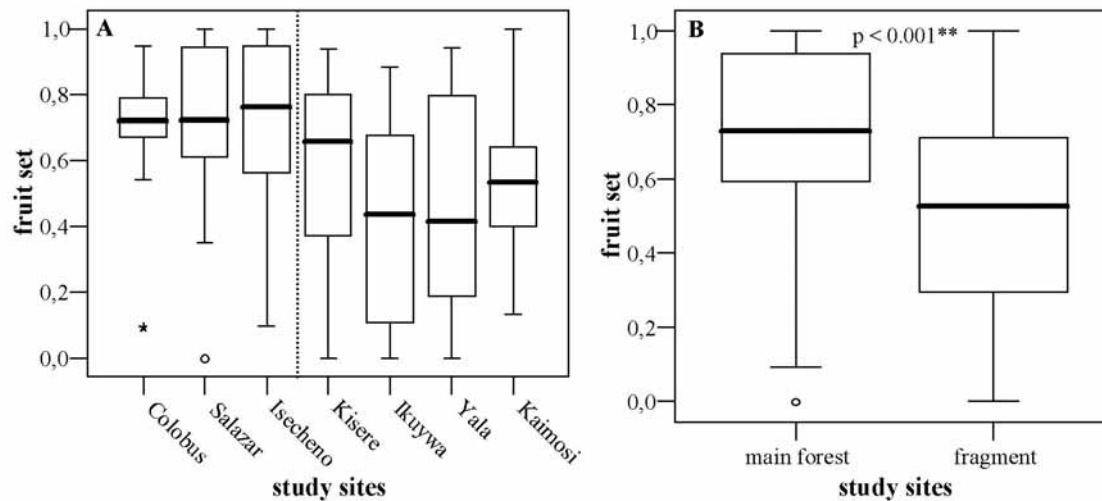


Fig. 17: Fruit set of *A. pubescens* (box plots):
 (A) in three main forest (left of the dashed line) and four forest fragment (right of the dashed line) study sites arranged from north to south,
 B) grouped in main forest (3) and forest fragment (4) study sites
 [(B) tested for differences by one-way ANOVA]

Regarding relevant biotic and abiotic factors, the final model ($R^2 = 0.110$) of a backward multiple regression stressed the size of the fragments ($p < 0.001^{**}$) as the most important factor influencing the fruit set of *A. pubescens* (Table 21; Fig. 18A).

Table 21: Final model coefficients of a backward multiple regression
 (started with $n=5$ factors; Appendix 15)

Factors	B	Standard error	Beta	t	R^2	Significance
(constant)	.493	.032		15.239	.110	< .001**
Size of forest fragments	2.534E-05	.000	.331	4.125		< .001**

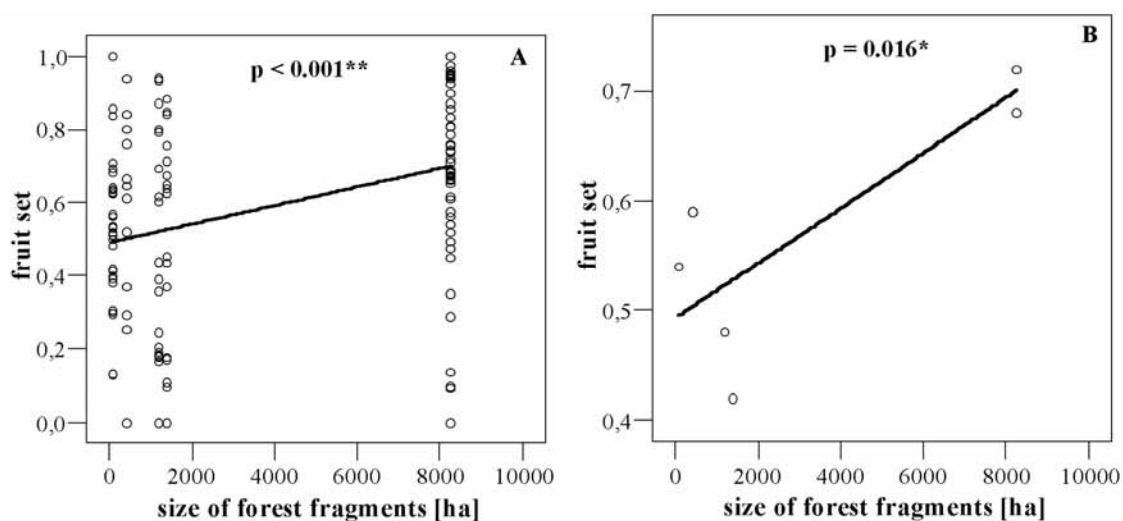


Fig. 18: Regression scatter plots *A. pubescens* fruit set:
 (A) fruit set to the factor size of forest fragments [ha],
 (B) fruit set of study sites to the factor size of forest fragments [ha]

The tendency of a higher fruit set in bigger forest islands became more obvious in a regression after grouping the data at study site level (Table 22; Fig. 18B).

Table 22: Regression coefficients

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.493	.038		12.878	.718	< .001**
Size of forest fragments	2.510E-05	.000	.847	3.567		.016*

6.1.4 Seed set

Out of 40 *A. pubescens* fruits from each study site, all seeds were counted and divided by the four potential ovules. The outcome was a mean seed set of 0.51 (SD: 0.13). All fruits contained at least one seed (seed set: 0.25). 2.5% (7) of the fruits developed the complete number of seeds (seed set: 1.00).

Table 23: Mean seed set (*A. pubescens*)

Study site	Seed set	(SD)
Colobus trail	0.49	0.12
Salazar	0.46	0.11
Isecheno	0.56	0.17
Kisere	0.51	0.08
Ikuywa	0.52	0.12
Yala	0.50	0.15
Kaimosi	0.55	0.14

Both the comparison of the mean seed set of the specific study sites and the grouped main forest (0.50/SD: 0.14) or forest fragment (0.52/SD: 0.13) study sites did not show significant differences (Table 23; Fig. 19A/B).

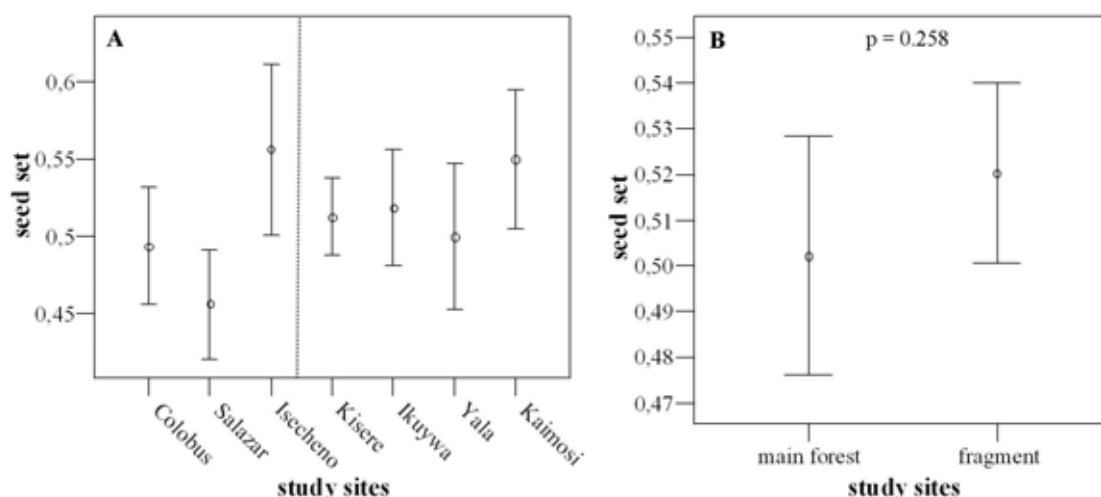


Fig. 19: Seed set of *A. pubescens* (error bars; standard error of mean value):
(A) in three main forest (left of the dashed line) and four forest fragment (right of the dashed line) study sites arranged from north to south,
(B) grouped in main forest (3) and forest fragment (4) study sites
[(B) tested for differences by one-way ANOVA]

An influence on the seed set of *A. pubescens* could be assumed due to a final model ($R^2=0.045$) of a backward multiple regression of collected biotic and abiotic factors. It displayed a rising regression ($p<0.001^{**}$) between the seed set and the paths inside the study sites per hectare (range: 0 – 18) (Table 24; Fig. 20A).

Table 24: Final model coefficients of a backward multiple regression (started with n=4 factors; Appendix 17)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.479	.012		39.521	.045	< .001**
Paths per ha	.004	.001	.212	3.615		< .001**

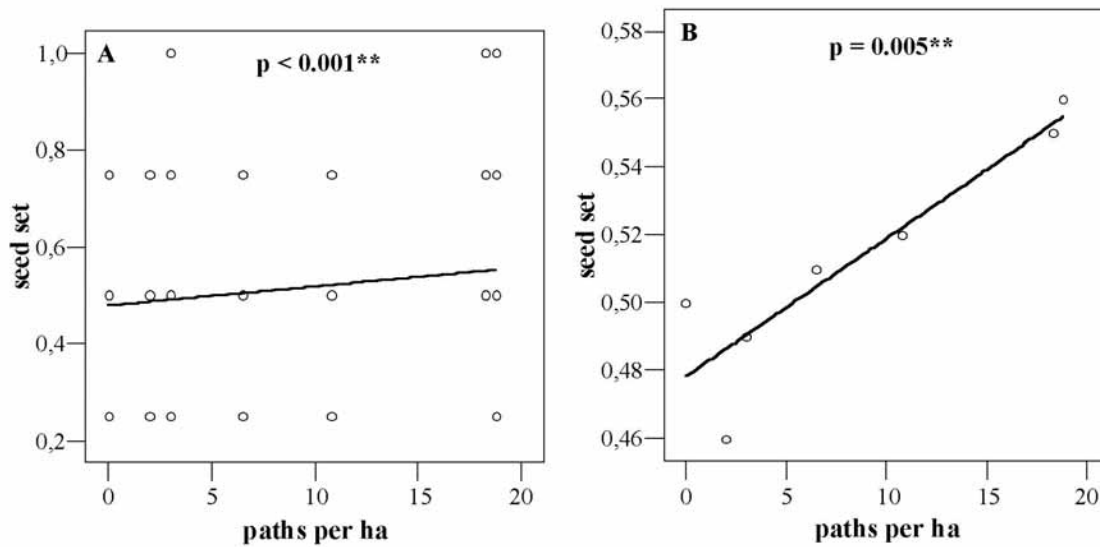


Fig. 20: Regression scatter plots of *A. pubescens* seed set:
 (A) seed set to the factor path per ha,
 (B) seed set of study sites to the factor path per ha

This tendency became more obvious after grouping the data on study site level (Fig.20B; Table 25).

Table 25: Regression coefficients

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.478	.009		51.761	.827	< .001**
Paths per ha	.004	.001	.909	4.885		.005**

6.1.5 Levels of pollination

Despite higher visitation frequencies inside forest fragment study sites (Fig. 21A); the number of pollen grains on stigmas was higher in main forest plots (Fig. 21B). In addition, the fruit set was again highly significant higher inside the main forest (Fig.21C), followed by higher seed set in forest fragment sites (Fig. 21D).

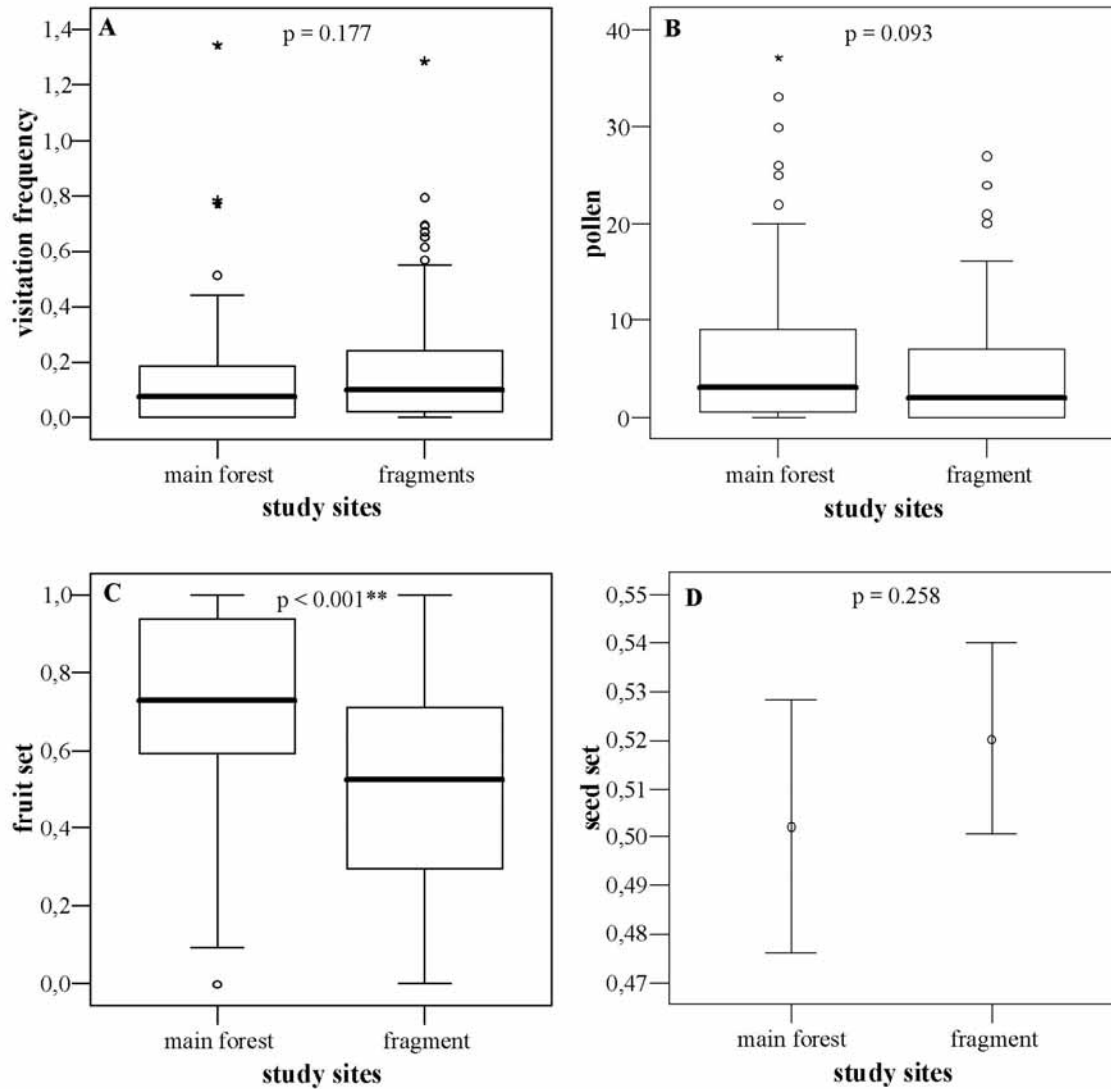


Fig. 21: Levels of pollination grouped in main forest and forest fragment study sites: (A) visitation frequencies, (B) pollen on stigmas, (C) fruit set, (D) seed set (*Acanthopale pubescens*)

6.2 *Acanthus eminens* [Acanthaceae]

Acanthus eminens flowers were observed between January 8 and January 25 2002 (subsequently called: campaign 2002) in three main forest study sites (Salazar I, Salazar II and Isecheno) and two forest fragment study sites (Kisere and Ikuywa). Between November 26, 2002 and January 11, 2003 (subsequently called: campaign 2003), four main forest sites (Colobus trail, Salazar I, Salazar II and Isecheno) and three forest fragment (Kisere, Ikuywa and Yala) were included in the study. In total, *A. eminens* was observed for 239 hours.

6.2.1 Visitation frequency

During both *A. eminens* campaigns, the following visitors were identified among others (Table 26/Table 27): *Xylocopa nigrita* [Xylocopinae]; the northern double-collared sunbird (*Nectarinia preussi*); the green-headed sunbird (*Nectarinia verticalis*); the variable sunbird (*Nectarinia venusta*); *Papilio bromius* Doubleday, 1845 [Papilionidae]; *Papilio phorcas* Cramer [1775] [Papilionidae]; *Papilio demodocus* Esper, [1798] [Papilionidae]; *Papilio lormieri neocrocea* Kocak, 1983 and *Cymothoe horbarti* Butler, 1899 [Nymphalidae].

In campaign 2002, 166 visitors were counted altogether during 71 observation units on 2449 observed flowers. The main visitor groups were carpenter bees (genus *Xylocopa*), followed by sunbirds and different sized butterflies (Table 26).

Table 26: Main visitor groups (campaign 2002)

Visitor group	n	% of all
<i>Xylocopa</i> bees	117	70.5
Vespidae	1	0.5
Lepidoptera	28	17
Nectarinidae	20	12

During campaign 2003, 341 visitors were counted on 1548 flowers monitored during 168 observation units. Throughout this second *A. eminens* campaign, the main visitor groups were carpenter bees, followed by other small to medium sized bees, different sized butterflies and sunbirds (Table 27).

Table 27: Main visitor groups (campaign 2003)

Visitor group	n	% of all
<i>Xylocopa</i> bees	185	54
other Apidae	108	32
Lepidoptera	36	11
Syrphidae, Diptera, Formicidae	4	1
Nectarinidae	8	2

Owing to pollinator effectiveness tests (Dietzsch, 2004) the *Xylocopa* bees appeared to be the most efficient pollinators of *A. eminens*. For this reason, only the *Xylocopa* bee visits will be considered in the subsequent analysis.

21.1% (15) of all observation units during campaign 2002 did not show any *Xylocopa* bee visit on *A. eminens* (Table 28). In campaign 2003, no *Xylocopa* bee visits were counted in 29.2% (49) of all the observation units (Table 29).

Table 28: Observation units without *Xylocopa* bee visits (*A. eminens*); campaign 2002

Study site	% of units without <i>Xylocopa</i> bee visit	Number of units (units without <i>Xylocopa</i> bee visit/ all units)
Salazar I	30	3/10
Salazar II	23.1	3/13
Isecheno	36.4	4/11
Kisere	18.8	3/16
Ikuywa	9.5	2/21

Table 29: Observation units without *Xylocopa* bee visits (*A. eminens*); campaign 2003

Study site	% of units without <i>Xylocopa</i> bee visit	Number of units (units without <i>Xylocopa</i> bee visit/ all units)
Colobus trail	60	6/10
Salazar I	33.3	6/18
Salazar II	19.6	9/46
Isecheno	54.2	13/24
Kisere	19.4	6/31
Ikuywa	20	4/20
Yala	26.3	5/19

In the *A. eminens* campaign 2002, a mean visitation frequency of 0.282 visits/flower/hour (SD: 0.35) was observed for all study sites. In contrast to this, a higher mean visitation frequency of 0.52 visits/flower/hour (SD: 0.77) was evident during the campaign 2003.

The main forest study site Salazar II showed the highest mean *Xylocopa* bee visitation frequency with 0.54 visits/flower/hour (SD: 0.62) concerning campaign 2002. Here, the lowest mean visitation frequency was found in the southernmost main forest study site Isecheno with 0.08 visits/flower/hour (SD: 0.10). When comparing the mean visitation frequency between the different study sites, no significant differences were apparent (Table 30; Fig. 22A).

Regarding campaign 2003, the newly integrated forest fragment Yala showed the highest mean *Xylocopa* bee visitation frequency with 0.86 visits/flower/hour (SD: 1.17), which means that statistically, almost every flower was visited by a *Xylocopa* bee during the observation units. The lowest mean visitation frequency of *Xylocopa* bees were found in the main forest study site Salazar I with 0.22 visits/flower/hour (SD: 0.33). However, no significant differences between mean visitation frequencies of all the study sites in general were apparent, as has already been observed for the *A. eminens* campaign 2002 (Table 31; Fig. 22B).

Table 30: Mean visitation frequencies
(*A. eminens*)

Study site (campaign 2002)	Visitation frequency	SD
Salazar I	0.14	0.11
Salazar II	0.54	0.62
Isecheno	0.08	0.10
Kisere	0.29	0.31
Ikuywa	0.30	0.18

Table 31: Mean visitation frequencies
(*A. eminens*)

Study site (campaign 2003)	Visitation frequency	SD
Colobus trail	0.37	0.57
Salazar I	0.22	0.33
Salazar II	0.56	0.64
Isecheno	0.30	0.59
Kisere	0.75	0.89
Ikuywa	0.37	0.77
Yala	0.86	1.17

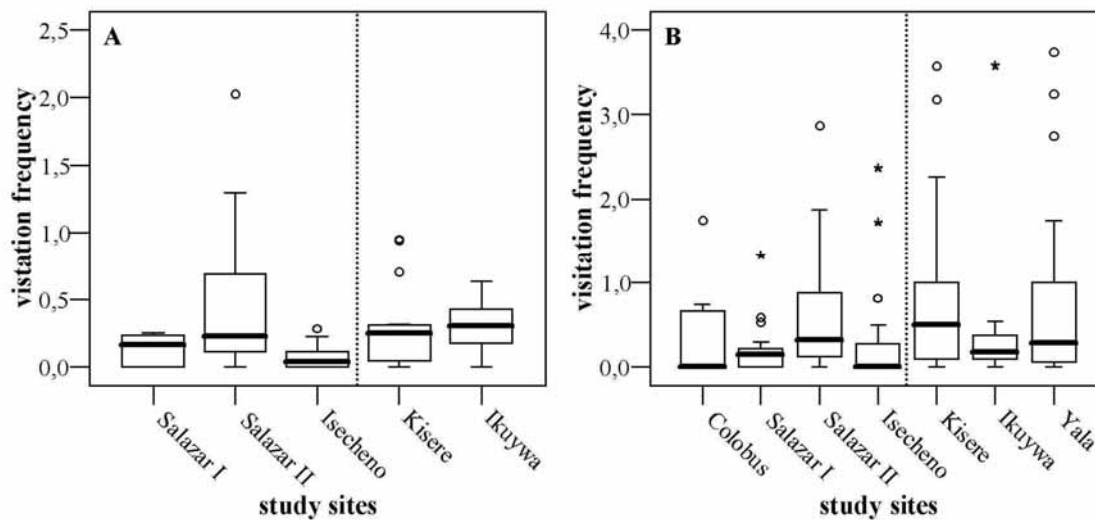


Fig. 22: Visitation frequencies of *Xylocopa* bees on *A. eminens* (box plots):
(A) in three main forest (left of the dashed line) and two forest fragment study sites (right of the dashed line) organized from north to south (campaign 2002),
(B) in four main forest study sites (left of the dashed line) and three surrounding forest fragment study sites (right of the dashed line) arranged from north to south (campaign 2003)

After grouping the study sites in main forest (campaign 2002: 0.27 visits/flower/hour, SD: 0.44; campaign 2003: 0.41 visits/flower/hour, SD: 0.58) and forest fragment (campaign 2002: 0.29 visits/flower/hour, SD: 0.24; campaign 2003: 0.67 visits/flower/hour, SD: 0.95) study sites, a tendency of higher visitation frequencies in forest fragment plots became evident (Fig. 23).

A significantly ($p=0.032^*$) lower visitation frequency of *Xylocopa* bees inside the main forest study sites could be shown during the campaign 2003 (Fig. 23B), where four main forest study sites were compared to three forest fragment study sites. Regarding the campaign 2002, non-significant ($p=0.800$) varieties between the visitation frequency of *Xylocopa* bees inside main forest and forest fragment study sites became evident (Fig. 23A).

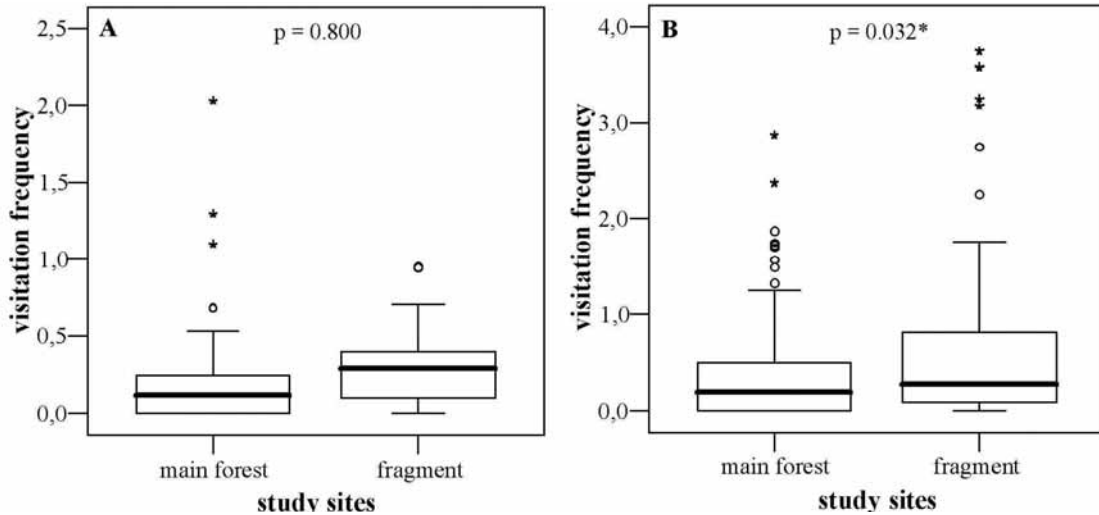


Fig. 23: Visitation frequencies of *Xylocopa* bees on *A. eminens* (box plots):
 (A) grouped in main forest (3) and forest fragment (2) study sites (campaign 2002),
 (B) grouped in main forest (4) and forest fragment (3) study sites (campaign 2003),
 [(A) and (B) tested for differences by one-way ANOVA]

A backward multiple regression of relevant biotic and abiotic factors concerning the *Xylocopa* bee visitation frequency during the campaign 2002 generated the final model ($R^2=0.125$) that both the cut tree per hectare ($p=0.025^*$) and the cloudiness ($p=0.024^*$) might influence the visitation frequency (Table 32).

Table 32: Final model (campaign 2002) coefficients of a backward multiple regression (started with n=4 factors; Appendix 19)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.184	.136		1.356	.125	.179
Cut trees per ha	-.028	.012	-.261	-2.292		.025*
Cloudiness	.146	.063	.263	2.310		.024*

Due to the very low rang of cloudiness (only between 0/8 and 3/8) between January 8 and January 25, 2002, this factor could be neglected due to its minor explanatory power. In contrast to this, *Xylocopa* visitation frequency became significantly lower the more trees per hectare were cut (range: 2 – 11) (Fig. 24A).

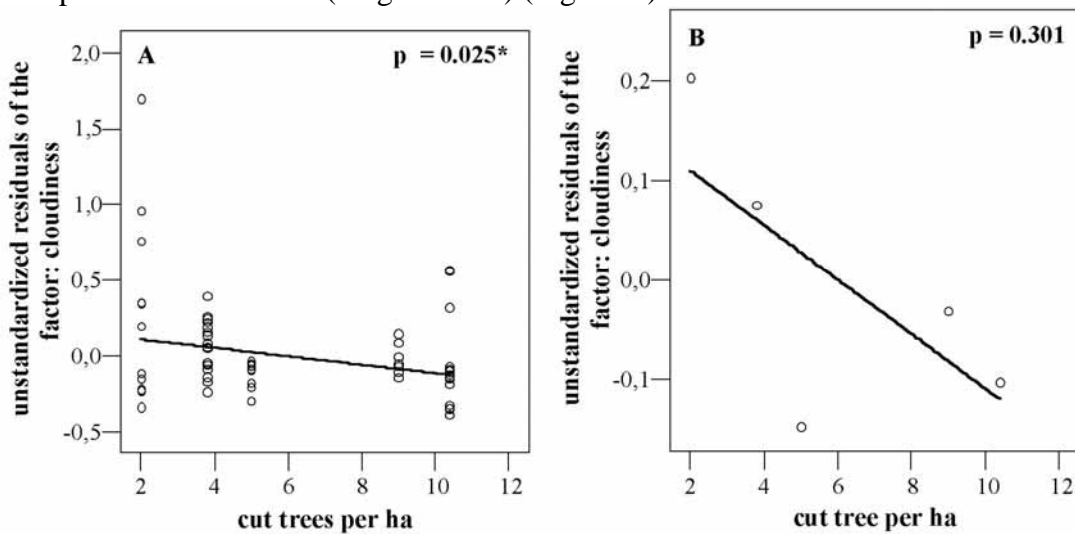


Fig. 24: Regression scatter plots of *A. eminens* (depend. variable= visitation frequencies):
 (A) cut trees per ha to unstandardized residuals of the factor cloudiness,
 (B) cut trees per ha of study sites to unstandardized residuals of the factor cloudiness

This potential influence of disturbance on the visitation frequencies became more obvious in a multiple regression model ($R^2=0.668$) after grouping the data on study site level (Fig. 24B; Table 33).

Table 33: Coefficients (campaign 2002) of a multiple regression (n=2 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.184	.236		.793	.668	.179
Cut trees per ha	-.028	.021	-.548	-1.343		.311
Cloudiness	.140	.101	.565	1.383		.301

Regarding campaign 2003, a backward multiple regression of relevant biotic and abiotic factors concerning the *Xylocopa* bee visitation frequency showed influences of two factors in the final model ($R^2=0.052$) namely cloudiness ($p=0.050^*$) and the size of the forest fragments ($p=0.062$) (Table 34).

Table 34: Final model (2003) coefficients of a backward multiple regression (started with n=3 factors; Appendix 20)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.840	.121		6.923	.052	< .001**
Cloudiness	-.075	.038	-.152	-1.975		.050*
Size of forest fragments	-3.04E-05	.000	-.145	-1.877		.062

Due to the wider range of cloudiness (between 0/8 and 7/8) and the significance of this regression, an inverse proportion effect could be assumed on the *Xylocopa* bee visitation behaviour (Fig. 25A). In general, it can be said that the more clouds there are the lower are the visitation frequencies.

In addition, higher visitation frequencies on *A. eminens* flowers became obvious in smaller forest fragments (Fig. 25B).

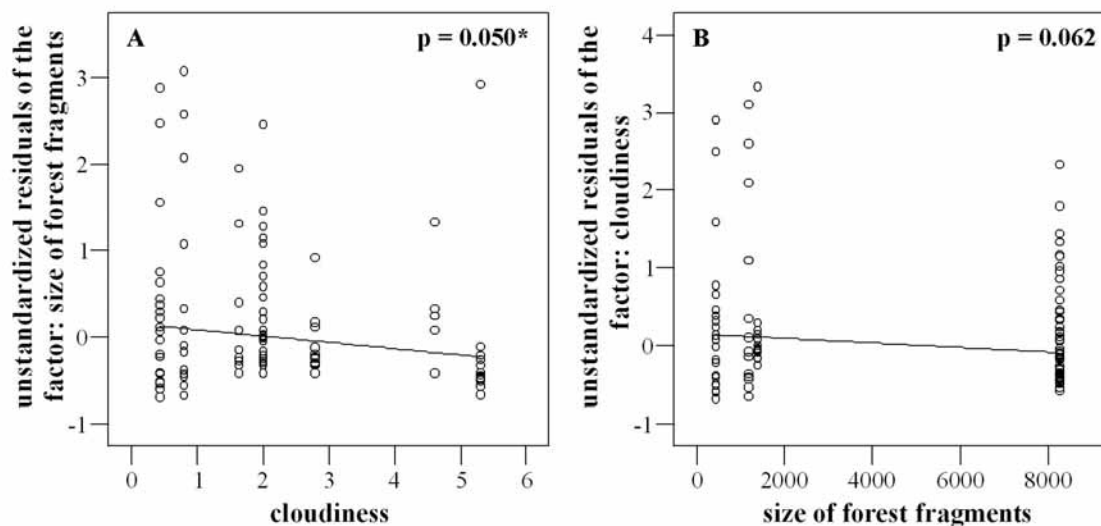


Fig. 25: Regression scatter plot of *A. eminens* (dependent variable= visitation frequencies): (A) cloudiness (eighth) to unstandardized residuals of the factor fragment size (B) forest fragment sizes to unstandardized residuals of the factor cloudiness

6.2.2 Primary pollination success

During the *A. eminens* campaign 2002, 225 stigmas were collected within the five study sites, distributed in Salazar I (47), Salazar II (53), Isecheno (27), Kisere (46), and Ikuywa (52). A further 335 stigmas were gathered in the campaign 2003, in Colobus trail (35), Salazar I (34), Salazar II (59), Isecheno (34), Kisere (64), Ikuywa (49), and Yala (60). After that, the pollen grains were counted under a fluorescence microscope (Fig. 26).

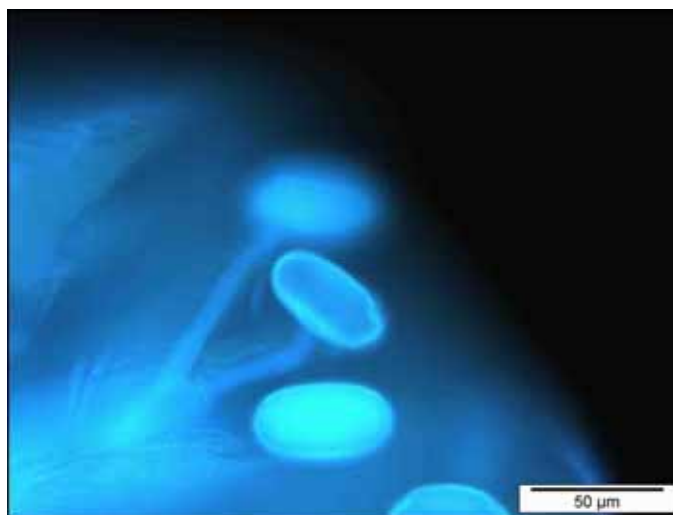


Fig. 26: *Acanthus eminens* [Acanthaceae] pollen connected with the stigma by pollen tubes

In campaign 2002, 34.2% (77 of 225) of all the investigated stigmas were loaded with pollen. The highest percentage of loaded stigmas was found in Salazar I with 53.2% (25 of 47), and the lowest in Ikuywa with 17.3% (9 of 52) (Table 35).

In contrast to this, the *A. eminens* campaign 2003 showed that 55% (186 of 338) of the stigmas were loaded with pollen. During this campaign, the highest percentage was found in Kisere with 68.7% (44 of 64) and the lowest in Salazar II with 32.2% (19 of 59) (Table 36).

Table 35: Percentage of stigmas loaded with pollen (*A. eminens*)

Study site (campaign 2002)	% of stigmas loaded with pollen	Number of stigmas
Salazar I	53.2	25/47
Salazar II	34	18/53
Isecheno	29.6	8/27
Kisere	37	17/46
Ikuywa	17.3	9/52

Table 36: Percentage of stigmas loaded with pollen (*A. eminens*)

Study site (campaign 2003)	% of stigmas loaded with pollen	Number of stigmas
Colobus trail	60	21/35
Salazar I	47.1	16/34
Salazar II	32.2	19/59
Isecheno	50	17/37
Kisere	68.7	44/64
Ikuywa	57.1	28/49
Yala	68.3	41/60

The maximum number of deposited pollen (50) on a stigma was found inside Salazar II during the campaign 2002 and in Isecheno during the campaign 2003 (90) respectively.

Yet, no significant differences were obvious with regard to the different study sites as concerns the mean pollen number on the stigmas during the *A. eminens* campaigns 2002 (Table 37; Fig. 27A) and 2003 (Table 38; Fig 27C).

Table 37: Mean pollen number per stigma (*A. eminens*)

Study site (campaign 2002)	Pollen number per stigma	SD
Salazar I	6.51	10.18
Salazar II	2.55	7.60
Isecheno	3.59	7.61
Kisere	2.44	4.89
Ikuywa	0.85	2.58

Table 38: Mean pollen number per stigma (*A. eminens*)

Study site (campaign 2003)	Pollen number per stigma	SD
Colobus trail	7.00	8.72
Salazar I	10.50	19.77
Salazar II	5.09	11.09
Isecheno	8.21	12.42
Kisere	9.84	12.65
Ikuywa	11.96	18.84
Yala	10.63	12.26

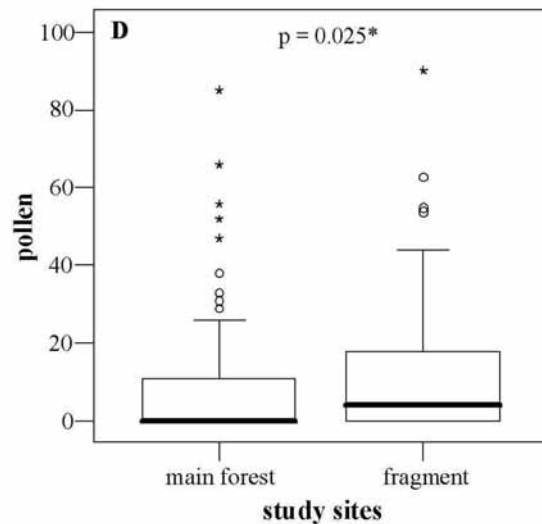
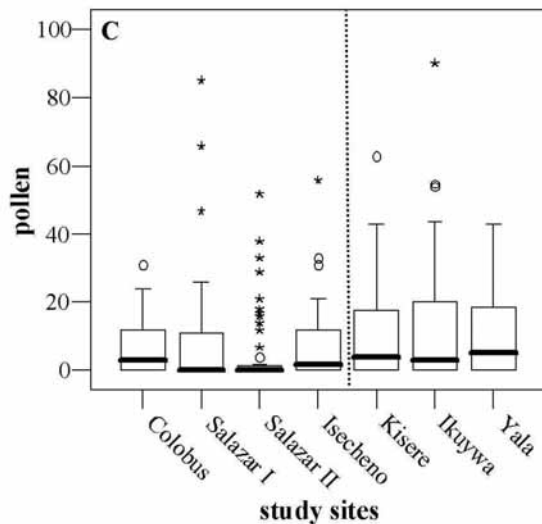
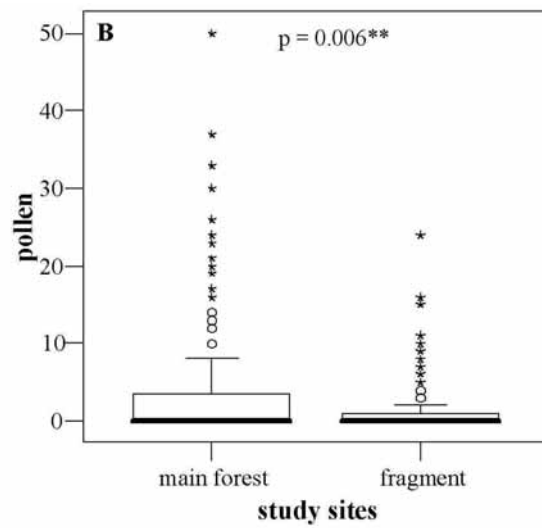
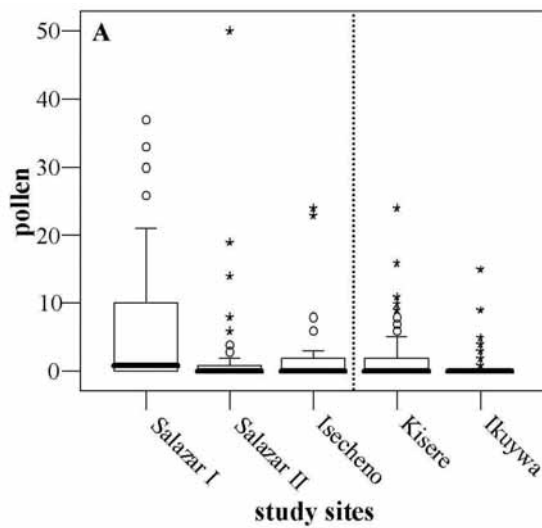


Fig. 27: Counted pollen on stigmas of *A. eminens* (box plots):
 (A) in three main forest (left of the dashed line) and two forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2002),
 (B) grouped in main forest (3) and forest fragment (2) study sites (campaign 2002),
 (C) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2003),
 (D) grouped in main forest (4) and forest fragment (3) study sites (campaign 2003),
 [(B) and (D) tested for differences by one-way ANOVA]

During the campaign 2002, however, the mean pollen deposit on *A. eminens* (3.08/SD: 7.18) was lower than during the campaign 2003 (9.06/SD: 14.00).

When grouping the counted pollen on the stigmas collected during the campaign 2002 in main forest (4.24/SD: 8.77) and forest fragment (1.59/SD: 3.90) study sites, a highly significant ($p=0.006^{**}$) lower mean number of pollen on stigmas was counted inside forest fragment study sites (Fig. 27B).

The percentage of stigmas loaded with pollen was also lower in forest fragments (Table 39).

Table 39: Percentage of stigmas loaded with pollen (*A. eminens*/ campaign 2002)

Study site	% of stigmas loaded with pollen	Number of stigmas (stigmas loaded with pollen/ all stigmas)
Main forest	40.2	51/127
Forest fragment	26.5	26/98

The opposite proportion was found concerning the counted pollen on stigmas in 2003. Here, significantly ($p=0.025^*$) fewer pollen could be detected on the stigmas of *A. eminens* in main forest study sites (7.29/SD: 13.28) as compared to forest fragment study sites (10.72/SD: 14.49) (Fig. 27D).

Here, the percentage of stigmas loaded with pollen was also lower in main forest plots (Table 40).

Table 40: Percentage of stigmas loaded with pollen (*A. eminens*/ campaign 2003)

Study site	% of stigmas loaded with pollen	Number of stigmas (stigmas loaded with pollen/ all stigmas)
Main forest	44.2	73/165
Forest fragment	65.3	113/173

Both the *A. eminens* campaign 2002 and 2003 showed a potential influence of the percentage of the forest in a buffer around the study sites on the number of deposited pollen on stigmas.

This could be indicated in the final model 2002 ($R^2=0.074$) of a backward multiple regression relating to the forest buffer of 2,000m (Table 41), and in the final model 2003 ($R^2=0.014$) to the forest buffer of 1,000m (Table 42).

Table 41: Final model (2002) coefficients of a backward multiple regression (started with n=5 factors; Appendix 22)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	-28.403	11.174		-2.542	.074	.012*
Protection status	9.620	4.217	.566	2.281		.023*
% of forest in a 2,000m buffer	.129	.044	.398	2.944		.004**
Plant species richness	.139	.051	.258	2.717		.007**
North-south gradient	-2.253	.862	-.452	-2.614		.010*

Table 42: Final model (2003) coefficients of a backward multiple regression (started with n=2 factors; Appendix 24)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	15.776	3.129		5.042	.014	< .001**
% of forest in a 1,000m buffer	-.104	.047	-.120	-2.213		.028*

The campaign 2002 showed a slight increase ($p=0.004^{**}$) in the number of pollen on stigmas in connection with a higher percentage of forest in a buffer of 2,000m (range: about 30% – 85%). The campaign 2003, however, showed a contrasting tendency, when a higher percentage of forest in a buffer of 1,000m (range: about 45% – 95%) resulted in a significant decrease ($p=0.028^*$) in the number of pollen on *A. eminens* stigmas.

Furthermore, the final model 2002 indicates that the protection status ($p=0.041^*$), the number of plant species (range: about 120 – 165) inside the study sites ($p=0.007^{**}$) and a north-south gradient were also potentially relevant factors. Here, higher number of pollen on stigmas were counted in forests which were less protected, highly diverse and located in the North.

In addition, self-pollination experiments showed an ability for autogamy (Dietzsch, 2004) (per. obser.).

6.2.3 Fruit set

During the two *Acanthus eminens* campaigns, 616 fruits were collected between January 26 and March 13, 2002 and December 13, 2002 to February 17, 2003. 156 fruits were gathered from 100 individuals during campaign 2002 (Salazar I (21); Salazar II (22); Isecheno (18); Kisere (19); Ikuywa (18); Yala (2)) and 460 fruits were collected from 127 individuals (Colobus trail (8); Salazar I (16); Salazar II (25); Isecheno (24); Kisere (26); Ikuywa (18); Yala (10)) in 2003.

During the campaign 2002, 70% (70) of the observed *A. eminens* individuals developed no fruits at all, while 38.6% (49) of the observed individuals showed a fruit set of zero in 2003. In contrast to this, 7% (7) of the observed individuals produced the maximum potential fruit number in 2002, but only 0.8% (1) in the campaign 2003. Instead, the mean fruit set appeared to be alike in both campaigns (2002: 0.13 (SD: 0.27); 2003: 0.14 (SD: 0.19)).

During both campaign, no significant differences concerning the mean fruit set between all study sites were obvious (Table 43; Table 44; Fig. 28A/C). Remarkable are only the high fruit set in Kisere with 0.47 (SD: 0.11) (campaign 2002) and the low fruit set in Salazar I with 0.01 (SD: 0.04) (campaign 2003).

Table 43: Mean fruit set (*A. eminens*)

Study site (campaign 2002)	Fruit set	SD
Salazar I	0.04	0.09
Salazar II	0.05	0.12
Isecheno	0.08	0.13
Kisere	0.47	0.45
Ikuywa	0.04	0.11
Yala	0.03	0.04

Table 44: Mean fruit set (*A. eminens*)

Study site (campaign 2003)	Fruit set	SD
Colobus trail	0.16	0.15
Salazar I	0.01	0.04
Salazar II	0.12	0.19
Isecheno	0.24	0.24
Kisere	0.10	0.16
Ikuywa	0.23	0.21
Yala	0.13	0.09

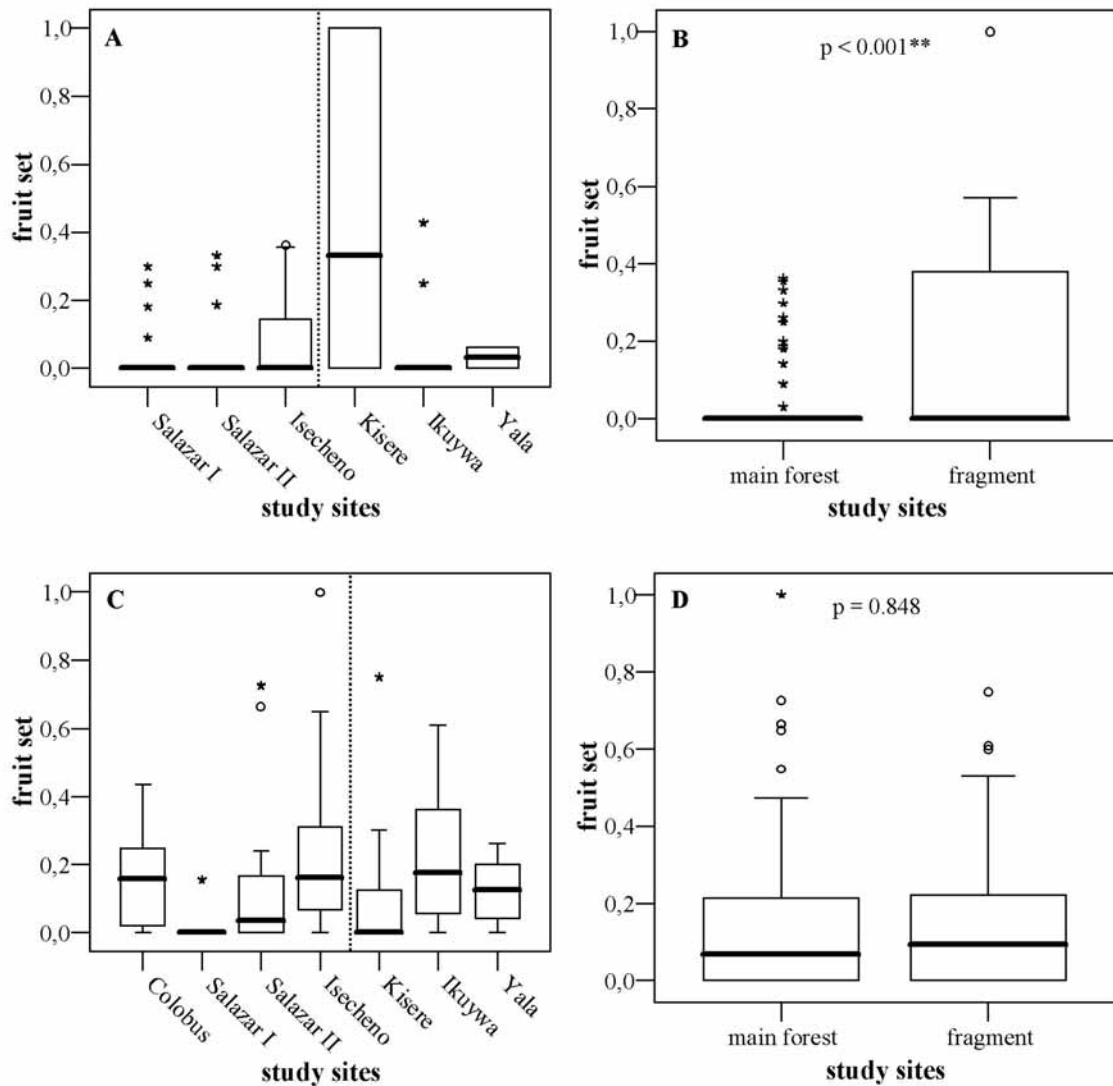


Fig. 28: Fruit set of *A. eminens* (box plots):

(A) in three main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2002),
 (B) grouped in main forest (3) and forest fragment (3) study sites (campaign 2002),
 (C) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2003),
 (D) grouped in main forest (4) and forest fragment (3) study sites (campaign 2003),
 [(B) and (D) tested for differences by one-way ANOVA]

The comparison of the grouped study sites in main forest (0.06/SD: 0.11) and forest fragments (0.25/SD: 0.39) showed a highly significant ($p < 0.001^{**}$) lesser fruit set of *A. eminens* inside the main forest plots (Fig. 28B) in campaign 2002.

In campaign 2003, a less high fruit set ($p = 0.848$) inside forest fragment (0.15/SD: 0.18) study sites was visible compared to main forest study sites (0.14/SD: 0.20) (Fig. 28D).

Regarding the campaign 2002 the final model ($R^2 = 0.349$) of a backward multiple regression showed a group of factors which might have a potential influence on the fruit set of *A. eminens*: cut trees per hectare ($p = 0.005^{**}$), percentage of forest in a buffer of 1,000m ($p = 0.096$), the north-south gradient ($p = 0.056$) and the C/N ratio of the soil ($p = 0.012^*$) (Table 45). All factors showed a proportional relation to the fruit set of *A. eminens*.

A higher fruit set was found in study sites surrounded by a higher percentage of forest in a buffer of 1,000m (range: 45% – 95%), which had a higher number of cut trees per hectare (range: 2 – 11), a higher C/N ratio in the soil (range: 5 – 10) and were situated in the southern parts of Kakamega Forest.

Table 45: Final model (campaign 2002) coefficients of a backward multiple regression (started with n=5 factors; Appendix 26)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	-3.470	1.555		-2.231	.349	.028*
% of forest in a 1,000m buffer	.009	.005	.567	1.680		.096
Cut trees per ha	.118	.041	1.388	2.860		.005**
North-south gradient	.192	.099	1.016	1.932		.056
C/N ratio	.210	.082	1.313	2.566		.012*

The final model ($R^2=0.132$) of a backward multiple regression concerning the campaign 2003 generated just two factors which had a potential influence on the fruit set of *A. eminens* (Table 46): On the one hand the protection status (nature reserve or forest reserve) ($p=0.001^{**}$) and on the other hand the percentage of forest in a buffer of 100m ($p<0.001^{**}$).

A higher fruit set was found inside forest reserve plots and in study sites surrounded by lesser forest in a buffer of 100m (range: 85% - 97%) (Fig. 29).

Table 46: Final model (campaign 2003) coefficients of a backward multiple regression (started with n=7 factors; Appendix 28)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	1.265	.337		3.749	.132	< .001**
Protection status	.165	.049	.302	3.382		.001**
% of forest in a 100m buffer	-.014	.004	-.332	-3.720		< .001**

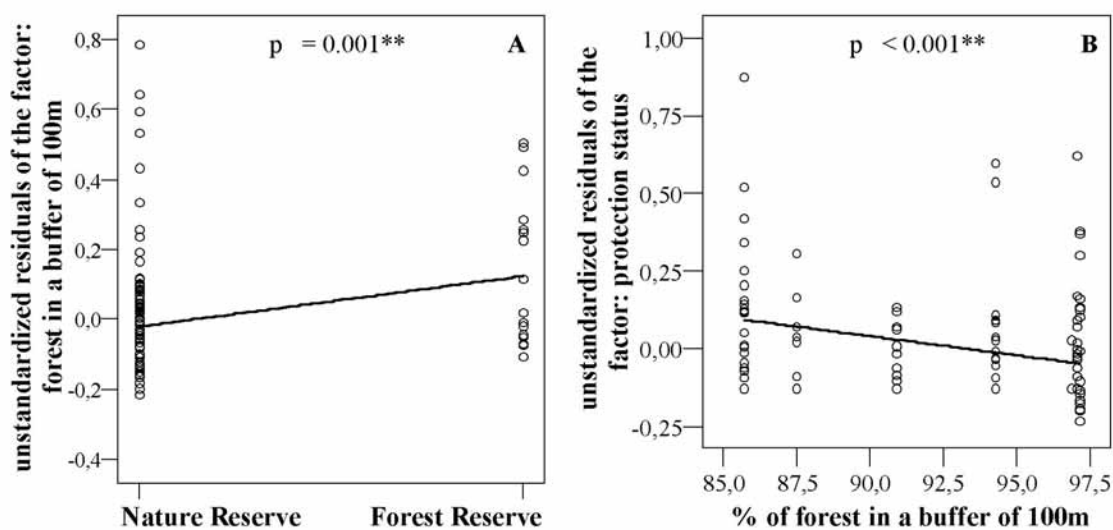


Fig. 29: Regression scatter plots *A. eminens* (campaign 2003); (dependent variable= fruit set): (A) protection status to unstandardized residuals of the factor forest in a buffer of 100m, (B) percentage of forest surrounding the observation areas in a buffer of 100m to unstandardized residuals of the factor protection status

A multiple regression on study site level (Table 47) confirmed and enhanced these significant tendencies (Fig. 30).

Table 47: Coefficients of a multiple regression (n=2 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	1.217	.332		3.663	.825	.022*
Protection status	.173	.048	.828	3.621		.022*
% of forest in a 100m buffer	-.014	.004	-.832	-3.638		.022*

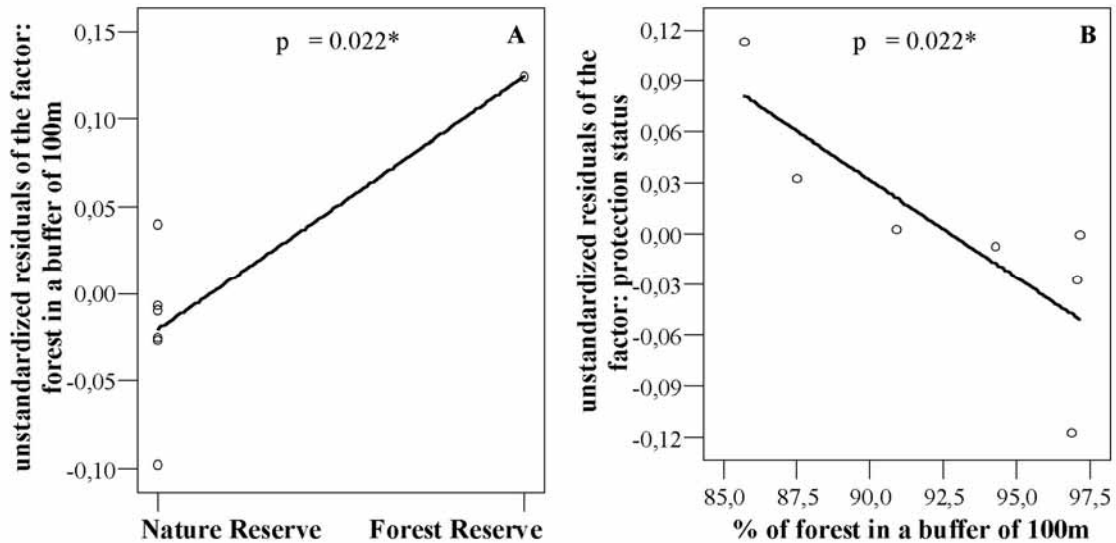


Fig. 30: Regression scatter plots A. *eminens* study sites (campaign 2003); (dep. varia.= fruit set): (A) protection status to unstandardized residuals of the factor forest in a buffer of 100m, (B) percentage of forest surrounding the observation areas in a buffer of 100m to unstandardized residuals of the factor protection status

6.2.4 Seed set

Out of 156 fruits collected in the campaign 2002 (Salazar I (8); Salazar II (9); Isecheno (26); Kisere (106); Ikuywa (6); Yala (1)), all the *A. eminens* seeds were counted and correlated with four potential ovules. The outcome of which was a mean seed set of 0.662 (SD: 0.33). Thus, 37.8% (59) of the observed fruits generated the maximum number of four seeds per fruit (seed set: 1.0), while 8.3% (13) of the fruits produced no seeds at all (seed set: 0).

In campaign 2003, all the seeds of the 430 collected fruits (Colobus trail (20); Salazar I (5); Salazar II (55); Isecheno (131); Kisere (38); Ikuywa (146); Yala (35)) were counted and correlated with the ovules. The result was a mean seed set of 0.586 (SD: 0.28). During this campaign, 16.5% (71) of the observed *A. eminens* fruits generated the maximum number of four seeds per fruit while no seeds at all were produced by 5.3% (23) of the fruits examined.

Both campaigns did not show significant differences with regard to the mean seed set of all study sites (Table 48; Table 49; Fig. 31 A/C).

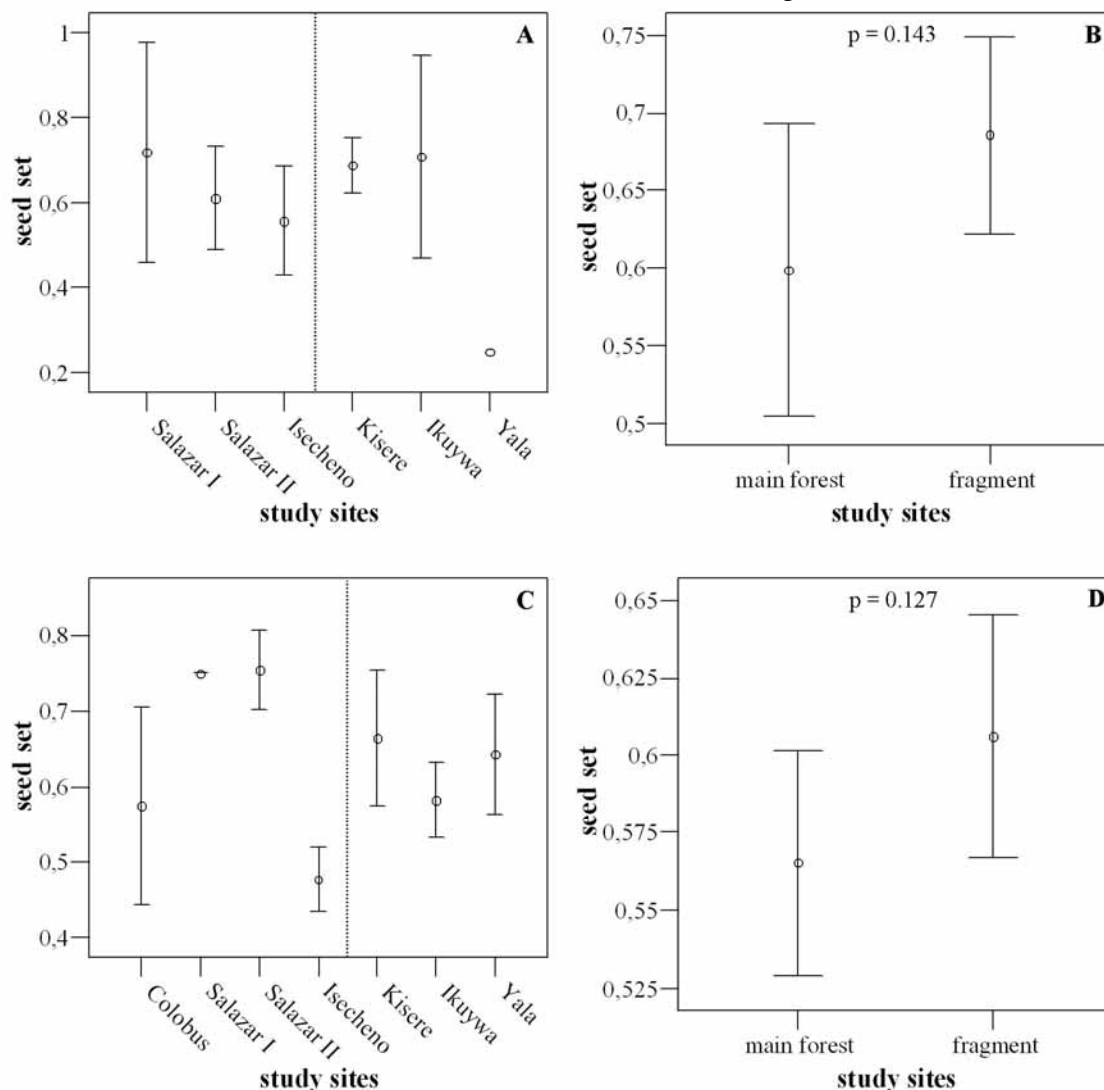
Table 48: Mean seed set (*A. eminens*)

Study site (campaign 2002)	Seed set	SD
Salazar I	0.72	0.36
Salazar II	0.61	0.18
Isecheno	0.56	0.33
Kisere	0.69	0.34
Ikuywa	0.71	0.29
Yala	0.25	-

Table 49: Mean seed set (*A. eminens*)

Study site (campaign 2003)	Seed set	SD
Colobus trail	0.58	0.29
Salazar I	0.75	0.00
Salazar II	0.76	0.20
Isecheno	0.48	0.24
Kisere	0.66	0.27
Ikuywa	0.58	0.31
Yala	0.64	0.24

The comparison of the grouped study sites of the campaign 2002 and 2003 revealed a non-significant (2002: $p=0.143$; 2003: $p=0.127$) higher mean seed set inside the forest fragment plots (2002: 0.69 (SD: 0.34); 2003: 0.61 (SD: 29)) compared to the main forest sites (2002: 0.60 (SD: 0.31); 2003: 0.57 (SD: 0.26)) (Fig. 31B/D).

**Fig. 31: Seed set of *A. eminens* (error bars; standard error of mean value):**

- (A) in three main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2002),
 (B) grouped in main forest (3) and forest fragment (3) study sites (campaign 2002),
 (C) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south (campaign 2003),
 (D) grouped in main forest (4) and forest fragment (3) study sites (campaign 2003),
 [(B) and (D) tested for differences by one-way ANOVA]

None of relevant biotic and abiotic factors expressed any correlation concerning the seed set of *A. eminens* in the Kakamega Forest during the field campaign 2002.

In contrast, the final model ($R^2=0.105$) of a backward multiple regression of the campaign 2003 showed a group of factors which have a potential influence on the seed set of *A. eminens* with regard to the percentage of forest in a buffer of 100m ($p=0.035^*$), the paths per hectare in the different study sites ($p=0.001^{**}$) and the pH-value of the soil ($p=0.027^*$).

Moreover, a higher *A. eminens* seed set was found in forest study sites which showed a higher percentage of forest in a buffer of 100m (range: 85% - 97%), less paths per hectare (range: 0 - 20) and higher pH-values in soils (range: 5.6 – 6.4) (Table 50).

Table 50: Final model (2003) coefficients of a backward multiple regression (started with n= factors; Appendix 30)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	-.657	.528		-1.245	.105	.214
% of forest in a 100m buffer	.007	.003	.124	2.114		.035*
Paths per ha	-.008	.002	-.199	-3.252		.001**
pH-value	.118	.053	.117	2.218		.027*

These tendencies became more obvious in a multiple regression model on study site level (Table 51; Fig. 32).

Table 51: Coefficients (2003) of a multiple regression (n=3 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	-.714	.293		-2.437	.958	.093
% of forest in a 100m buffer	.008	.003	.390	3.096		.053
Paths per ha	-.008	.002	-.510	-3.906		.030*
pH-value	.108	.032	.422	3.319		.045*

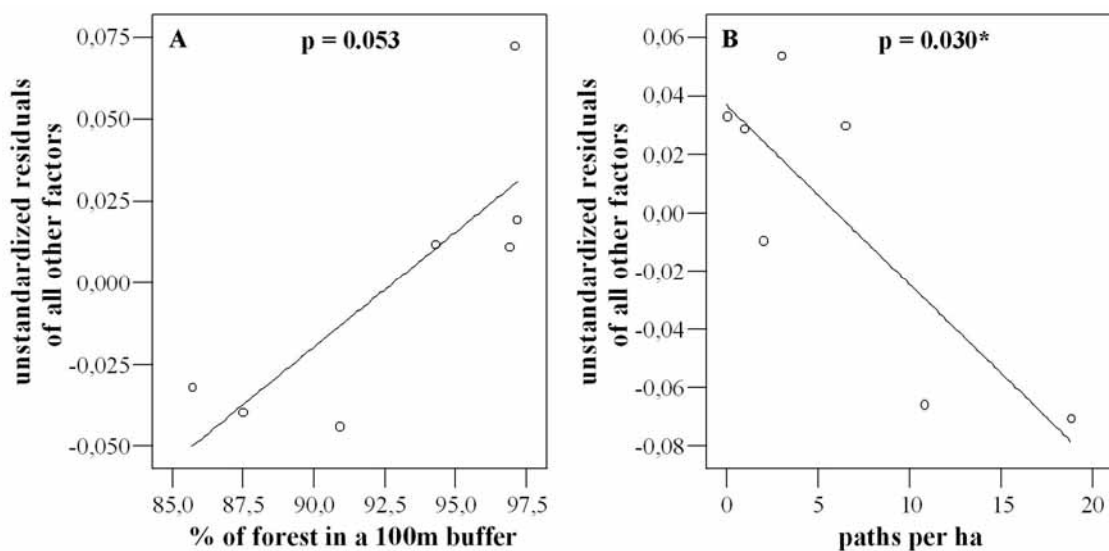


Fig. 32: Regression scatter plots *A. eminens* study sites (campaign 2003); (dep. varia. = seed set): (A) percentage of forest surrounding the observation areas in a buffer of 100m to unstandardized residuals of the factors paths per ha and pH-value of the soils, (B) paths per hectare to unstandardized residuals of the factors percentage of forest surrounding the observation areas in a buffer of 100m and pH-value of the soils

6.2.5 Levels of pollination

Regarding campaign 2002, the higher visitation frequency inside forest fragments (Fig.A) wasn't consequentially leading to a higher number of pollen on stigmas (Fig.B). In contrast to this, higher fruit and seed sets (Fig.C/D) were found in forest fragment sites again.

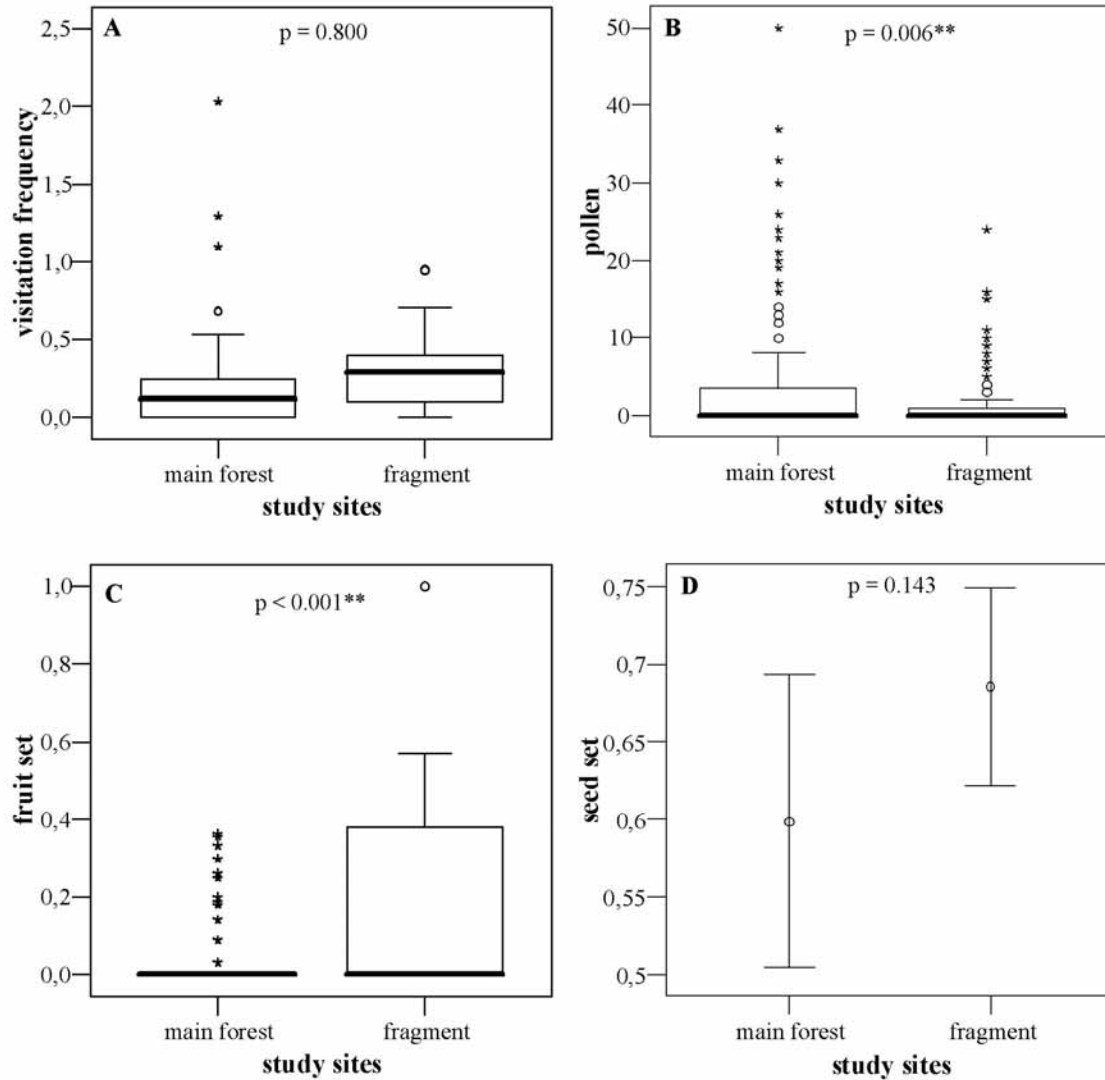


Fig. 33: Levels of pollination grouped in main forest and forest fragment study sites: (A) visitation frequencies, (B) pollen on stigmas, (C) fruit set, (D) seed set (*Acanthus eminens*/ campaign 2002)

In campaign 2003, all levels of pollination were higher in forest fragment study sites: visitation frequencies (Fig. 34A), number of pollen on stigmas (Fig. 34B), percentage of stigmas loaded with pollen, fruit and seed set (Fig. 34C/D).

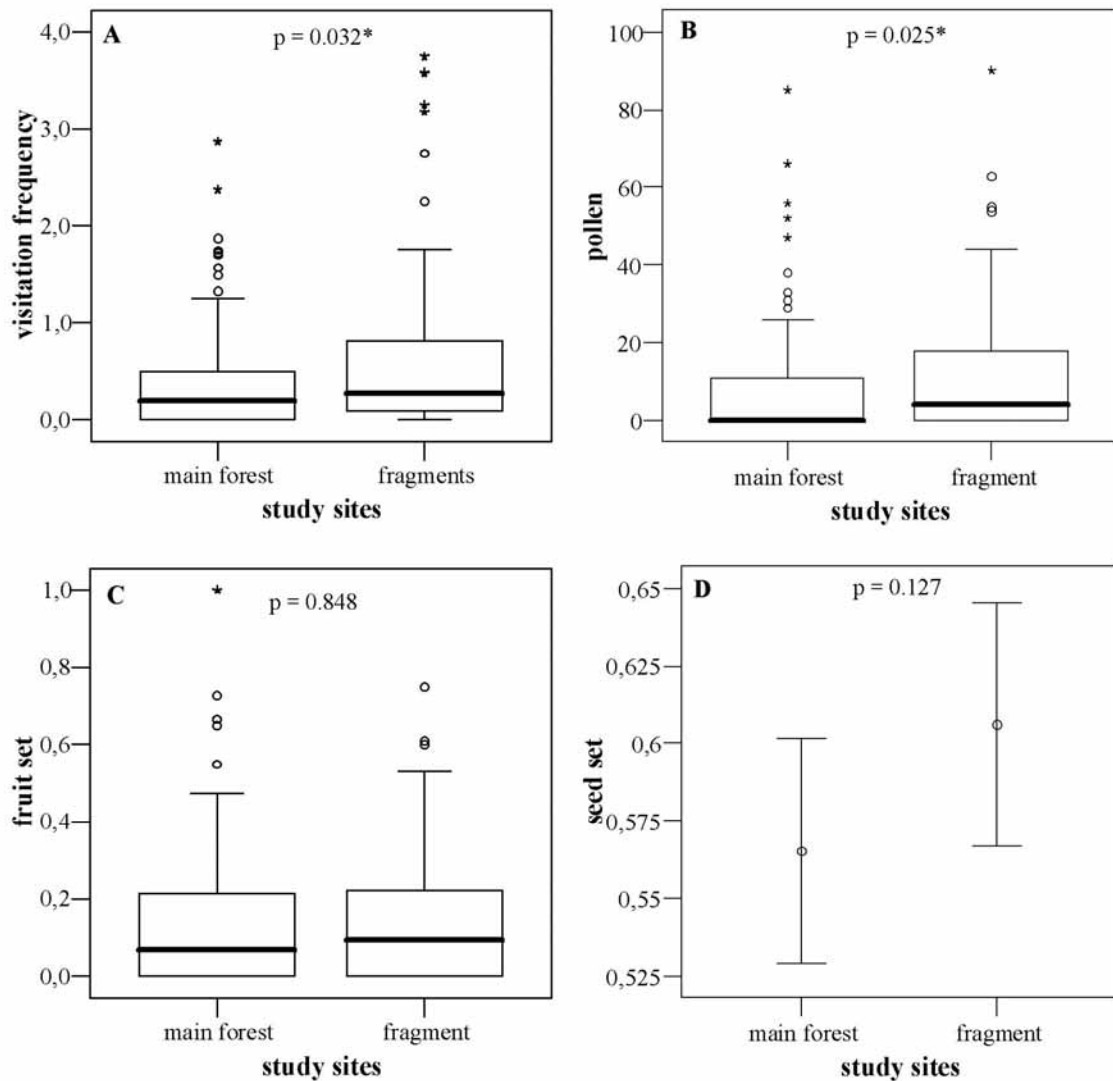


Fig. 34: Levels of pollination grouped in main forest and forest fragment study sites: (A) visitation frequencies, (B) pollen on stigmas, (C) fruit set, (D) seed set (*Acanthus eminens*/ campaign 2003)

6.3 *Heinsenia diervilleoides* [Rubiaceae]

6.3.1 Visitation frequency

Between November 19, 2002 and January 20, 2003 *H. diervilleoides* trees were observed in four main forest (Colobus trail, Buyangu hill, Salazar I and Isecheno) and three forest fragment study sites (Malawa, Kisere and Yala). All in all, 1260 visits were counted during 152 observation units on 3278 flowers. The main visitor group was bees (1185/94%), here divided into the three subgroups small to medium sized bees (mainly Halictids and Megachilids), honey bees (*Apis mellifera*) and carpenter bees (genus *Xylocopa*). Apart from bees, just a few visits by different sized butterflies and several wasps, could be observed on the *H. diervilleoides* flowers (Table 52).

Table 52: Main visitor groups

Visitor group	n	% of all
<i>Apis mellifera</i>	132	10.5
<i>Xylocopa</i> bees	8	0.6
other Apidae	1045	83
Lepidoptera	9	0.7
Nematocera, Diptera, Formicidae, Coleoptera, Heteroptera, Vespidae	66	5.2

Due to the tiny flowers of *H. diervilleoides*, the long duration of the visits of all visitor groups (averages more than 10 seconds) and their behaviour inside the flowers – multiple touching of the stigmas all visitors were included in the following analysis to be a potential pollinator.

In 11.8% (18) of all observation units, no visits were detected (Table 53).

Table 53: Observation units without visits (*H. diervilleoides*)

Study site	% of units without visit	Number of units (units without visit/ all units)
Colobus trail	40	10/25
Buyangu hill	10	1/10
Salazar I	15	3/20
Isecheno	10	2/20
Malawa	10	2/20
Kisere	0	0/37
Yala	0	0/20

The mean visitation frequency of *H. diervilleoides* flowers was 1.17 visits/flower/hour (SD: 1.57), which means that statistically every flower was visited at least once in each observation unit (!). The highest mean visitation frequency of 2.08 visits/flower/hour (SD: 1.82) was observed inside the northern forest fragment Kisere while the northernmost study site inside the main forest Colobus trail showed the lowest mean visitation frequency of 0.33 visits/flower/hour (SD: 0.55).

Between the mean visitation frequency of all the study sites, no significant differences were apparent (Table 54; Fig. 35A).

Table 54: Mean visitation frequencies (*H. diervilleoides*)

Study site	Visitation frequencies	SD
Colobus trail	0.33	0.55
Buyangu hill	1.23	0.92
Salazar I	0.49	0.69
Isecheno	2.02	2.69
Malawa	0.70	0.58
Kisere	2.08	1.82
Yala	0.78	0.51

Higher visitation frequencies in forest fragment study sites (1.38 visits/flower/hour, SD: 1.48) compared to main forest (0.94 visits/flower/hour, SD: 1.64) study sites were found ($p=0.086$) in *H. diervilleoides* populations (Fig. 35B).

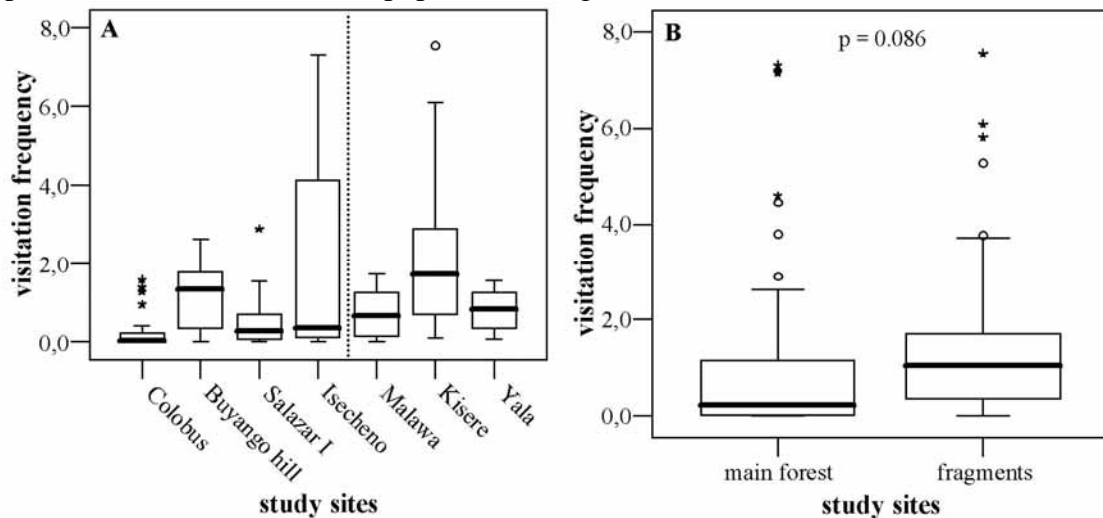


Fig. 35: Visitation frequencies on *H. diervilleoides* (box plots) of all visitors: (A) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south, (B) grouped in main forest (4) and forest fragment (3) study sites [tested for differences by one-way ANOVA]

Owing to the final backward multiple regression model ($R^2=0.202$), which included relevant biotic and abiotic factors, an influence of the two factors - cut trees per hectare and succession stages of forest study sites - could be shown concerning the visitation frequency of *H. diervilleoides* (Table 55).

Table 55: Final model coefficients of a backward multiple regression (started with $n=5$; Appendix 32)

Factors	B	Standard error	Beta	t	R^2	Significance
(constant)	.627	.400		1.566	.202	.119
Cut trees per ha	.175	.036	.361	4.926		< .001**
Succession stages	-.318	.093	-.250	-3.408		.001**

In a range from 2 to 13 cut trees per hectare, highly significant ($p<0.001^{**}$) lower visitation frequencies became apparent in less disturbed forest study sites. In addition, highly significant higher visitation frequencies ($p=0.001^{**}$) were found in near-primary or old secondary forest plots respectively in contrast to middle-aged secondary or heavily logged and planted forest study sites (Fig. 36).

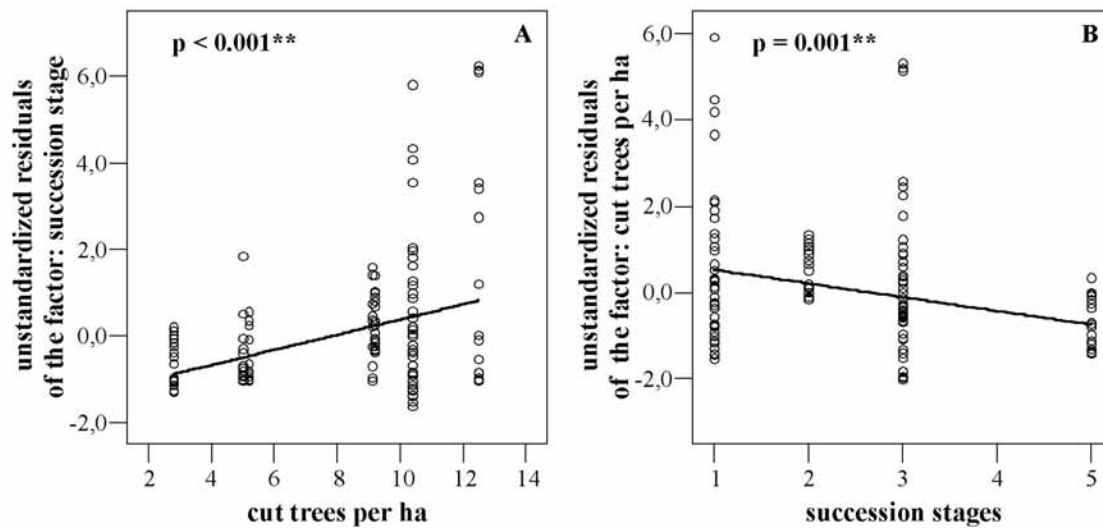


Fig. 36: Regression scatter plots *H. diervilleoides* (dependent variable= visitation frequencies):
(A) cut trees per hectare to unstandardized residuals of the factor succession stages of study sites,
(B) succession stages (1=near-primary; 2=old secondary; 3= middle-aged secondary; 4=young secondary; 5=heavily logged and planted) to unstandardized residuals of the factor cut trees per hectare

These tendencies became more obvious in a multiple regression after grouping the data at study site level (Table 56; Fig. 37).

Table 56: Coefficients of a multiple regression (n=2 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.668	.284		2.352	.939	.078
Cut trees per ha	.175	.026	.851	6.856		.002**
Succession stages	-.327	.073	-.557	-4.488		.011*

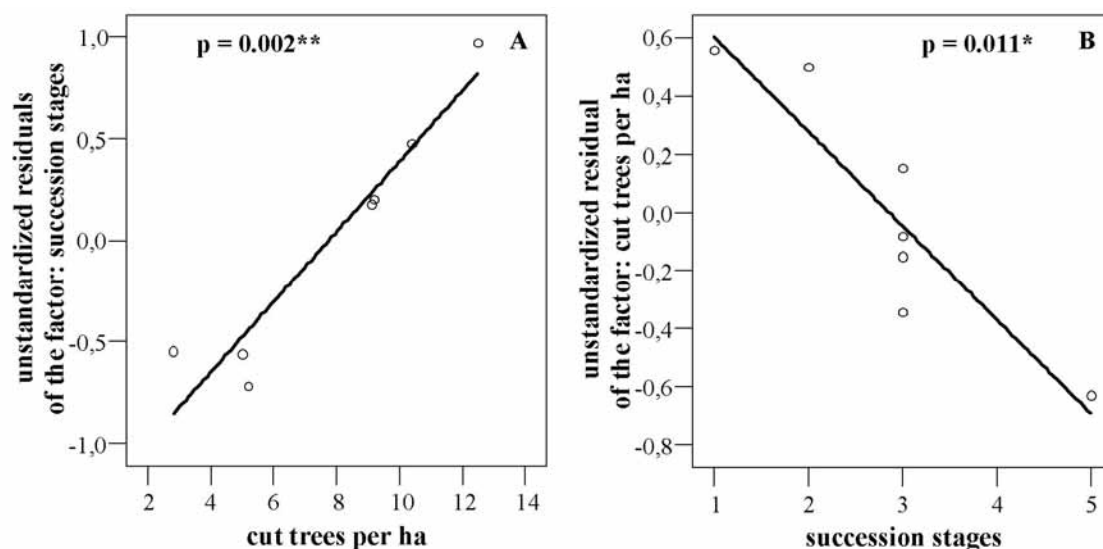


Fig. 37: Regression scatter plots *H. diervilleoides* study sites (dep. variable= visitation frequencies):
(A) cut trees per hectare to unstandardized residuals of the factor succession stages of the main forest and forest fragments study site areas,
(B) succession stages (1=near-primary; 2=old secondary; 3= middle-aged secondary; 4=young secondary; 5=heavily logged and planted) to unstandardized residuals of the factor cut trees per hectare

6.3.2 Primary pollination success

Inside the seven *H. diervilleoides* study sites, 224 stigmas were collected in the sites Colobus trail (62), Buyangu hill (15), Salazar I (5), Isecheno (45), Malawa (59), Kisere (9) and Yala (29). After that, the pollen grains were counted in a defined apical region (from the region upwards where the stigma splits) under a fluorescence microscope (Fig. 38).

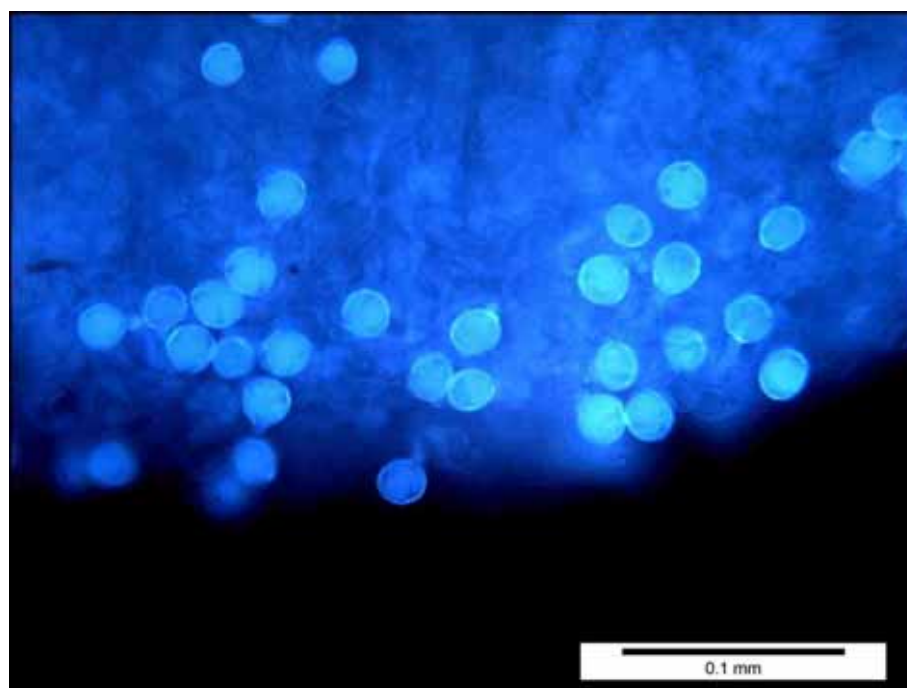


Fig. 38: *Heinsenia diervilleoides* [Rubiaceae] pollen on the stigma (sporadic pollen tubes visible)

The maximum number of deposited pollen in a defined apical region (1289) on a stigma was found inside the study site at the Buyangu hill. In addition, pollen grains were found on 99.6% of all researched stigmas; just one stigma at Salazar I was not loaded.

The 224 collected stigmas of *H. diervilleoides* showed a mean pollen number per stigma - in a defined apical region - of 328.05 (SD: 266.96). Nevertheless, no significant differences regarding the mean pollen number per stigma were found in the diverse study sites (Table 57; Fig. 39A). The low mean number of pollen on stigmas in Yala (94.90 (SD: 140.35)), however, appeared to be conspicuous when compared to the highest pollen counts at Buyangu hill (648.73 (SD: 319.58)).

Table 57: Mean pollen number per stigma (*H. diervilleoides*)

Study site	Pollen number per stigma (defined apical region)	SD
Colobus trail	480.05	250.46
Buyangu hill	648.73	319.58
Salazar I	352.60	241.61
Isecheno	237.64	182.11
Malawa	264.86	213.88
Kisere	350.22	268.42
Yala	94.90	140.35

The counted pollen on stigmas grouped in main forest (409.06/SD: 274.03) and forest fragment (221.97/SD: 216.65) study sites described a highly significant ($p < 0.001^{**}$) lower mean number of pollen on stigmas inside the forest fragment study sites (Fig.39B).

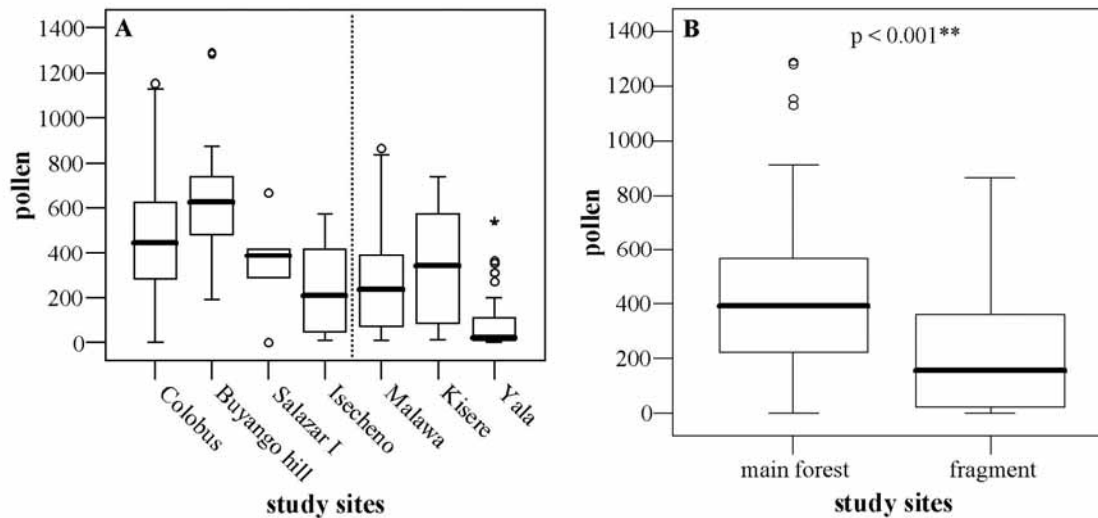


Fig. 39: Counted pollen on stigmas of *H. diervilleoides* (box plots):
 (A) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (4) and forest fragment (3) study sites
 [tested for differences by one-way ANOVA]

The final model ($R^2=0.320$) of a backward multiple regression showed a group of factors which have a potential influence on the number of pollen deposited on the stigmas of *H. diervilleoides*. These factors are the size of the forest fragments ($p < 0.001^{**}$), the abundance of the *H. diervilleoides* individuals ($p=0.051$), the pH-value of the soil ($p=0.014^*$), the percentage of forest in a buffer of 100m ($p=0.015^*$) and the protection status ($p=0.007^{**}$). With the exception of the pH-value, all other factors showed a proportional relation concerning the counted pollen on stigmas (Table 58).

A higher number of pollen was found in larger forest fragments, in more abundant *H. diervilleoides* populations, on soils with a higher pH-value (range: 5.0 – 6.5), in less protected areas and in study sites which were surrounded by a higher percentage of forest in a buffer of 100m (range: 70% – 98%).

Table 58: Final model coefficients of a backward multiple regression (started with n=7 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	247.069	524.281		.471	.320	.638
Size of forest fragments	.041	.007	.596	5.665		< .001 ^{**}
Abundance of <i>H. diervilleoides</i>	20.118	10.273	.172	1.958		.051
pH-value	-172.807	70.064	-.178	-2.466		.014 [*]
% of forest in a 100m buffer	6.630	2.703	.213	2.453		.015 [*]
Protection status	194.189	71.080	.321	2.732		.007 ^{**}

Self-pollination experiments showed no ability for autogamy as none of nine manipulated flowers of the tested individuals ($n=3$) produced any seeds.

6.3.3 Fruit set

Between January 22 and March 03, 2003, 1483 fruits of *H. diervilleoides* were collected. All in all, the fruit set of 128 marked individuals was classified in the regions Colobus trail (18), Buyangu hill (12), Salazar I (6), Isecheno (26), Malawa (14), Kisere (38) and Yala (14).

To sum up, 15.6% (20) of the observed individuals developed no fruits at all while the maximum possible fruit number (fruit set: 1.0) was achieved by 8.6% (11). During this campaign *H. diervilleoides* showed a mean fruit set of 0.40 (SD: 0.33).

When comparing the fruit set of all study sites, no significant differences were obvious apart from a general tendency of a higher mean fruit set inside forest fragment plots compared to the main forest study sites (Table 59; Fig. 40A).

Table 59: Mean fruit set (*H. diervilleoides*)

Study site	Fruit set	(SD)
Colobus trail	0.25	0.21
Buyangu hill	0.15	0.22
Salazar I	0.62	0.25
Isecheno	0.22	0.19
Malawa	0.39	0.32
Kisere	0.61	0.34
Yala	0.48	0.33

However, when grouping the study sites in main forest (0.25/SD: 0.24) and forest fragment sites (0.54/SD: 0.34), the prior assumption could be verified as *H. diervilleoides* produced highly significant ($p < 0.001^{**}$) more fruits in the forest fragment study sites (Fig. 40B).

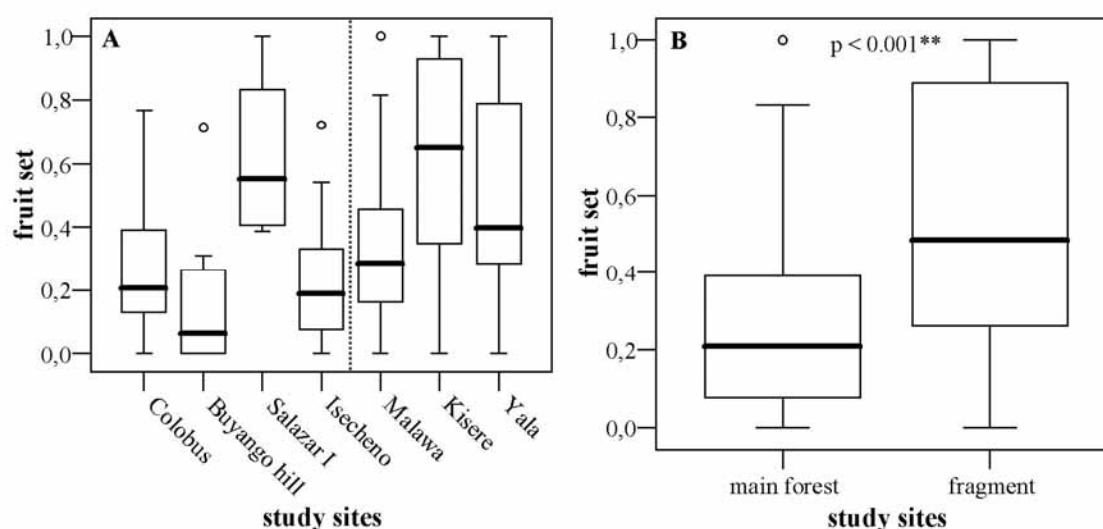


Fig. 40: Fruit set of *H. diervilleoides* (box plots):
 (A) in four main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (4) and forest fragment (3) study sites
 [tested for differences by one-way ANOVA]

The final model ($R^2=0.250$) of a backward multiple regression showed the following group of factors which had a potential influence on the fruit set of *H. diervilleoides*: the percentage of forest in a buffer of 100m ($p=0.008^{**}$), the succession stages of the observed study sites ($p=0.001^{**}$), humidity ($p=0.001^{**}$) and a north-south gradient ($p=0.001^{**}$) (Table 60).

A higher fruit set was found in study sites that were surrounded by a higher proportion of forest in a 100m buffer (range: 70% – 98%) and in older successional forest stages. It could also be observed in study sites with higher humidity (range: 45% – 85%) and a more northward location.

Table 60: Final model coefficients of a backward multiple regression (started with n=5 factors; Appendix 36)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	-.973	.486		-2.003	.250	.047*
% of forest in a 100m buffer	.010	.004	.336	2.702		.008**
Succession stages	-.168	.048	-.629	-3.509		.001**
Humidity	.022	.007	.990	3.298		.001**
North-south gradient	-.138	.040	-.856	-3.418		.001**

6.3.4 Seed set

Out of 1483 collected fruits (Colobus trail (181), Buyangu hill (36), Salazar I (103), Isecheno (228), Malawa (324), Kisere (513) and Yala (98)), all seeds were counted and divided by two potential ovules. The outcome was a mean seed set of 0.39 (SD: 0.37). In addition, 34.1% (506) of the observed *H. diervilleoides* fruits generated the potential maximum number of two seeds per fruits (seed set: 1.0), while 8.2% (122) of the fruits produced no seed (seed set: 0) at all, and merely three fruits were found containing three seeds.

When comparing the mean seed set of all study sites, no obvious significant differences were apparent (Table 61; Fig. 41A).

Table 61: Mean seed set (*H. diervilleoides*)

Study site	Seed set	(SD)
Colobus trail	0.30	0.33
Buyangu hill	0.25	0.35
Salazar I	0.44	0.35
Isecheno	0.29	0.36
Malawa	0.45	0.35
Kisere	0.43	0.39
Yala	0.45	0.33

When study sites grouped in main forest (0.32/SD: 0.35) and forest fragment (0.44/SD: 0.37) plots a highly significant ($p<0.001^{**}$) lower seed set in main forest sites could be shown (Fig. 41B).

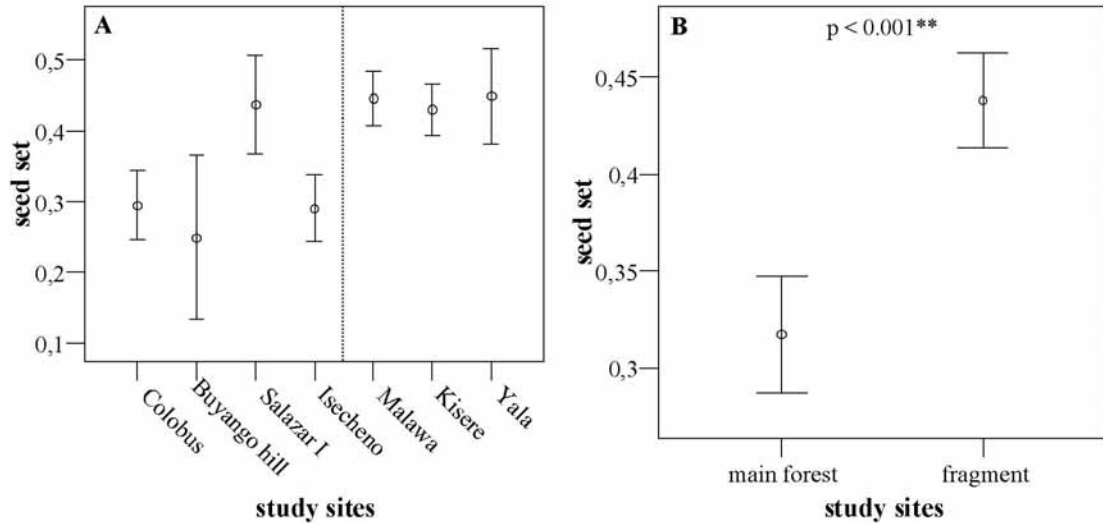


Fig. 41: Seed set of *H. diervilleoides* (error bars; standard error of mean value):
(A) in four main forest (left of the dashed line) and three forest fragment
(right of the dashed line) study sites arranged from north to south,
(B) grouped in main forest (4) and forest fragment (3) study sites
[tested for differences by one-way ANOVA]

With low evidence, the final model ($R^2=0.035$) of a backward multiple regression indicated the following group of factors which might have a potential influence on the seed set of *H. diervilleoides* (Table 62) the abundance of *H. diervilleoides* individuals inside the forest fragments ($p < 0.001^{**}$), the percentage of forest in a buffer of 100m ($p = 0.001^{**}$), a north-south gradient ($p = 0.033^*$), the size of the forest fragments ($p < 0.001^{**}$) and $[Mg^{++}]$ of the soil ($p = 0.042^*$).

Here, a lower seed set was found in study sites with more abundant *H. diervilleoides* populations that were surrounded by a lower proportion of forest in a 100m buffer (range: 70% – 98%), located more southwards in larger forest fragments and with lower $[Mg^{++}]$ in the soil (range: 10 – 55 $mmol_c \cdot kg^{-1}$).

Table 62: Final model coefficients of a backward multiple regression
(started with n=5 factors; Appendix 38)

Factors	B	Standard error	Beta	t	R^2	Significance
(constant)	-.193	.227		-.853	.035	.394
Abundance of <i>H. diervilleoides</i>	-.026	.007	-.251	-3.494		< .001**
% of forest in a 100m buffer	.009	.003	.245	3.250		.001**
North-south gradient	-.021	.010	-.113	-2.137		.033*
Size of forest fragments	-1.79E-05	.000	-.187	-5.190		< .001**
$[Mg^{++}]$ in the soil	.004	.002	.114	2.031		.042*

6.3.5 Levels of pollination

Despite higher visitation frequencies inside forest fragment study sites (Fig. 42A), the number of pollen on stigmas was higher in main forest plots (Fig. 42B). In contrast to this, both the fruit and the seed set were significantly higher in forest fragment sites again (Fig. 42C/D).

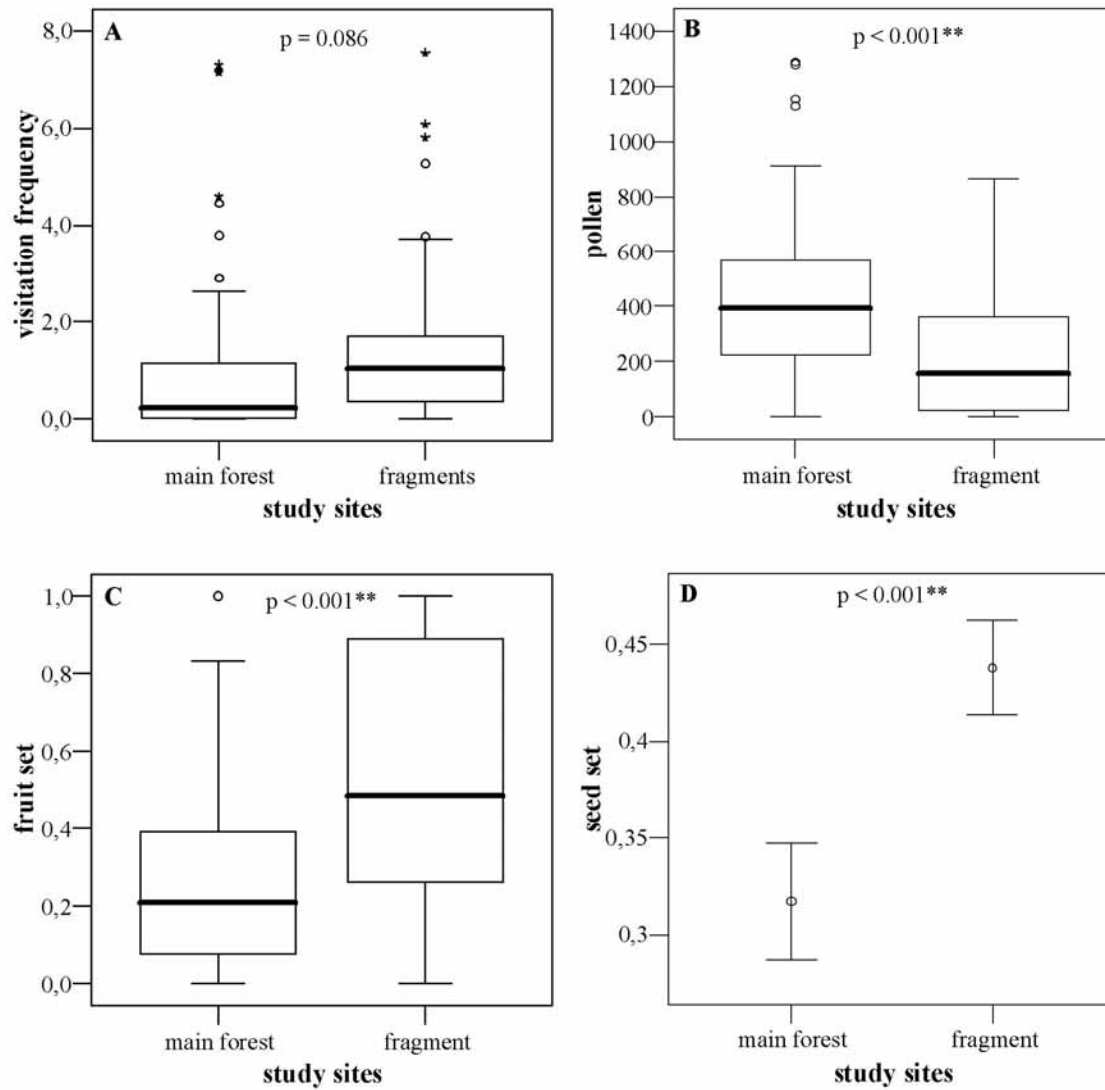


Fig. 42: Levels of pollination grouped in main forest and forest fragment study sites: (A) visitation frequencies, (B) pollen on stigmas, (C) fruit set, (D) seed set (*Heinsenia diervilleoides*)

6.4 *Dracaena fragrans* [Ruscaceae]

6.4.1 Flower visitation

Both the flower architecture and the intensive odour spread at night led to the hypothesis that *D. fragrans* might be pollinated by moths.

Covering experiments – from 6 a.m. to 6 p.m. (= flowers not covered with light netting at night) and from 6 p.m. to 6 a.m. (= flowers not covered with light netting during the day) - corroborated this assumption, because a highly significant ($p < 0.001^{**}$) lower number of pollen was counted on stigmas exposed to possible visitors during the day as compared to flowers that were not covered at night (Fig. 43). In addition, some night-flying Lepidoptera stuck on the covering bags that were clammy from the thaw in the early morning.

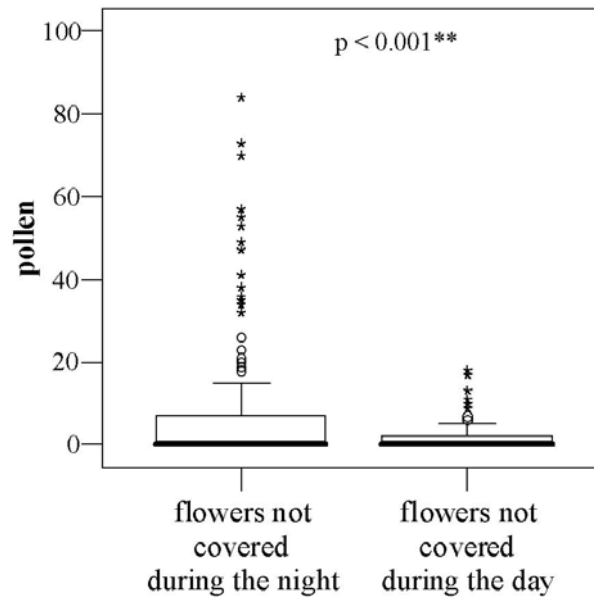


Fig. 43: Counted pollen on stigmas on *D. fragrans* in a night/day flower covering experiment [tested for differences by one-way ANOVA]

Because the *Dracaena fragrans* flowers were mainly visited at night, no visitation frequency data that was relevant for its pollination could be recorded in this study.

6.4.2 Primary pollination success

In the six *D. fragrans* study sites, 145 stigmas were collected, distributed in Colobus trail (45), Isecheno (38), Malawa (18), Kisere (35) and Ikuywa (9). Following collection, the pollen grains were counted under a fluorescence microscope (Fig. 44).

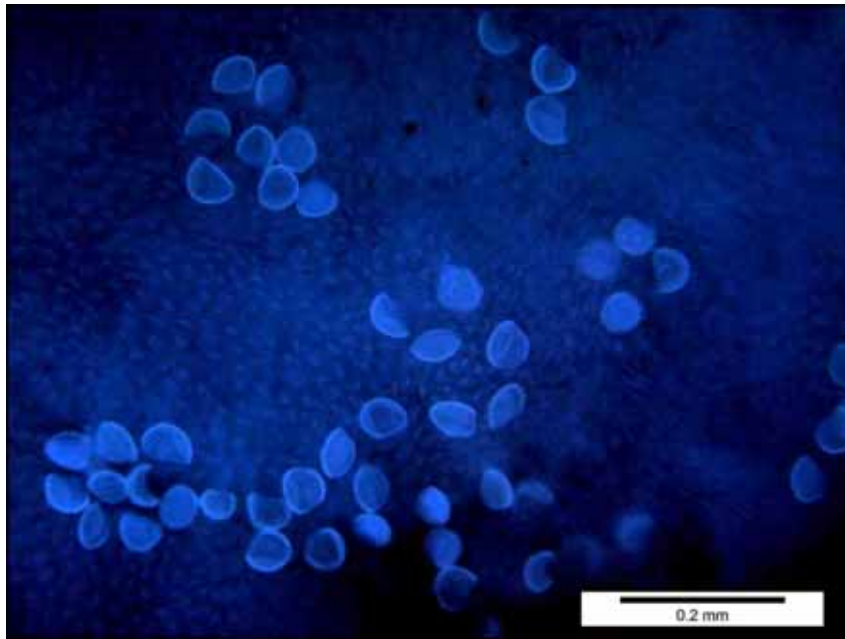


Fig. 44: *Dracaena fragrans* [Ruscaceae] pollen on the stigma

82.8% (120 of 145) of all examined stigmas were loaded with at least one pollen. The highest percentage of loaded stigmas was found at Colobus trail with 97.8% (44 of 45), while the lowest was found in Malawa with 27.8% (5 of 18) (Table 63).

Table 63: Percentage of stigmas loaded with pollen (*D. fragrans*)

Study site	% of stigmas loaded with pollen	Number of stigmas
Colobus trail	97.8	44/45
Isecheno	97.4	37/38
Malawa	27.8	5/18
Kisere	80	28/35
Ikuywa	66.7	6/9

The collected 145 *D. fragrans* stigmas showed a mean pollen number of 43.16 (SD: 67.09). The maximum number of deposited pollen (469) was found inside the study site in Isecheno. When comparing the mean pollen number per stigma of all different study sites a higher number of pollen in main forest study sites became evident (Table 64; Fig.45A).

Table 64: Mean pollen number per stigma (*D. fragrans*)

Study site	Pollen number per stigma	SD
Colobus trail	44.71	58.51
Isecheno	95.05	88.64
Malawa	2.78	9.62
Kisere	10.54	16.18
Ikuywa	23.89	54.68

Consequently, pollen counts on stigmas grouped in main forest (67.76/SD: 77.58) and forest fragment (10.23/SD: 24.65) study sites revealed a highly significant ($p < 0.001^{**}$) lower mean number of pollen on stigmas inside the forest fragment study sites (Fig.45B).

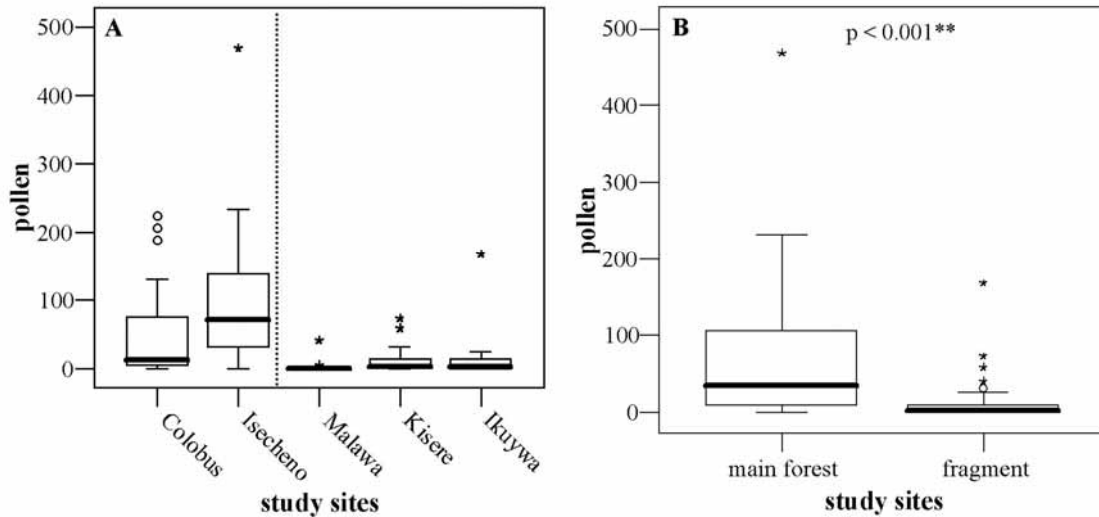


Fig. 45: Counted pollen on stigmas of *D. fragrans* (box plots):
 (A) in two main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (2) and forest fragment (3) study sites
 [tested for differences by one-way ANOVA]

The percentage of stigmas loaded with pollen was also lower in forest fragments (Table 65).

Table 65: Percentage of stigmas loaded with pollen (*D. fragrans*)

Study site	% of stigmas loaded with pollen	Number of stigmas (stigmas loaded with pollen/ all stigmas)
Main forest	97.6	81/83
Forest fragment	62.9	39/62

A north-south gradient ($p=0.070$), humidity ($p<0.001^{**}$) and the protection status ($p=0.003^{**}$) turned out in the final model ($R^2=0.266$) of a backward multiple regression to be potential factors which might influence the number of pollen deposited on the stigmas of *D. fragrans* (Table 66).

The higher the humidity (range: 45% – 80%) and the higher the protection of the forest fragments, the higher was the number of pollen found there. In addition, less pollen were counted on stigmas which were collected further north.

Table 66: Final model coefficients of a backward multiple regression (started with $n=8$ factors; Appendix 40)

Factors	B	Standard error	Beta	t	R^2	Significance
(constant)	-54.789	27.866		-1.966	.266	.051
North-south gradient	9.618	5.274	.160	1.824		.070
Humidity	1.891	.453	.356	4.171		< .001**
Protection status	-39.496	13.163	-.230	-3.000		.003**

Self-pollination experiments showed an ability for autogamy as 44% ($n=9$) of the tested plant individuals produced at least one seed. But these seeds looked poorer and smaller than regular pollinated ones.

6.4.3 Fruit set

2430 fruits of *D. fragrans* were collected between August 26, 2002 and March 31, 2003. In total, the fruit set of 83 marked individuals was classified the regions Colobus trail (20), Isecheno (20), Malawa (17), Kisere (20), and Ikuywa (6).

The examination showed that 34.9% (29) of the observed individuals developed no fruits at all and that the maximum fruit number (fruit set: 1.0) had not been achieved. During this campaign *D. fragrans* showed a mean fruit set of 0.14 (SD: 0.15).

In addition, no significant differences in fruit set became evident when examining the study sites individually (Table 67; Fig. 46A).

Table 67: Mean fruit set (*D. fragrans*)

Study site	Fruit set	(SD)
Colobus trail	0.19	0.16
Isecheno	0.12	0.09
Malawa	0.17	0.22
Kisere	0.10	0.14
Ikuywa	0.09	0.05

A division into main forest (0.15/SD: 0.132) and forest fragment (0.13/SD: 0.17) study sites did not show any significant differences as well ($p=0.444$) concerning the mean fruit sets (Fig. 46B).

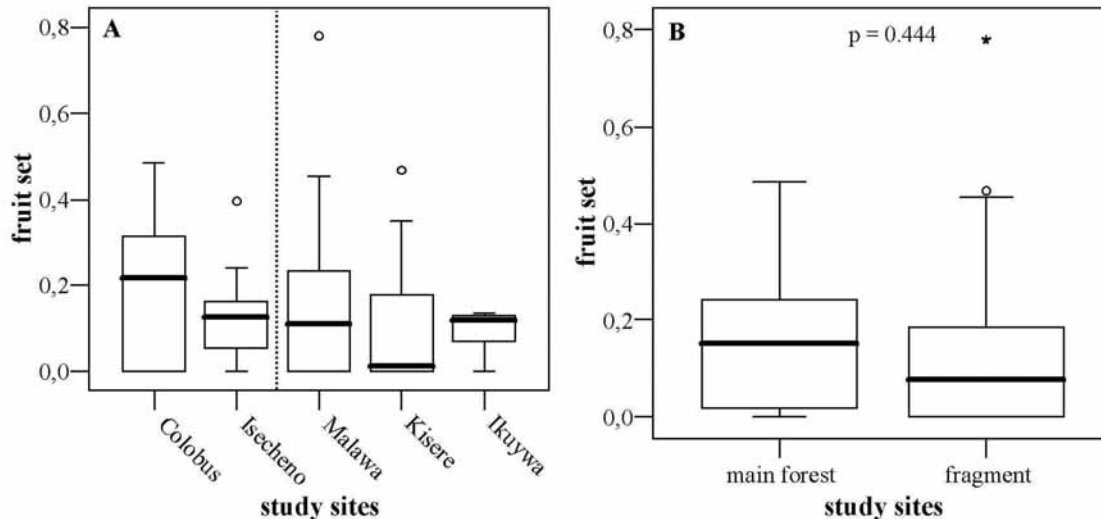


Fig. 46: Fruit set of *D. fragrans* (box plots):
 (A) in two main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (2) and forest fragment (3) study sites
 [tested for differences by one-way ANOVA]

None of relevant biotic and abiotic factors showed any correlation regarding the fruit set of *D. fragrans* in Kakamega Forest during this field campaign.

6.4.4 Seed set

Out of 2413 collected fruits (Colobus trail (615), Isecheno (566), Malawa (318), Kisere (347), Ikuywa (164) and Yala (403)) all the seeds were counted and correlated with three possible ovules, the outcome of which was a mean seed set of 0.17 (SD: 0.24). 2.2% (52) of the observed *D. fragrans* fruits generated the maximum number of three seeds per fruit (seed set: 1.0), while 62.1% (1498) of the fruits examined produced no seeds at all (seed set: 0).

With the exception of Yala (0.47/SD: 0.28), the mean seed set of *D. fragrans* showed no significant differences with regard to the different study sites (Table 68; Fig. 47A).

Table 68: Mean seed set (*D. fragrans*)

Study site	Seed set	(SD)
Colobus trail	0.11	0.18
Isecheno	0.05	0.12
Malawa	0.17	0.21
Kisere	0.14	0.21
Ikuywa	0.09	0.15
Yala	0.47	0.28

When grouping the study sites in main forest (0.08/SD: 0.16) and forest fragment (0.25/SD: 0.28) plots, a significantly higher ($p < 0.001^{**}$) seed set in the forest fragment sites were visible (Fig. 47B).

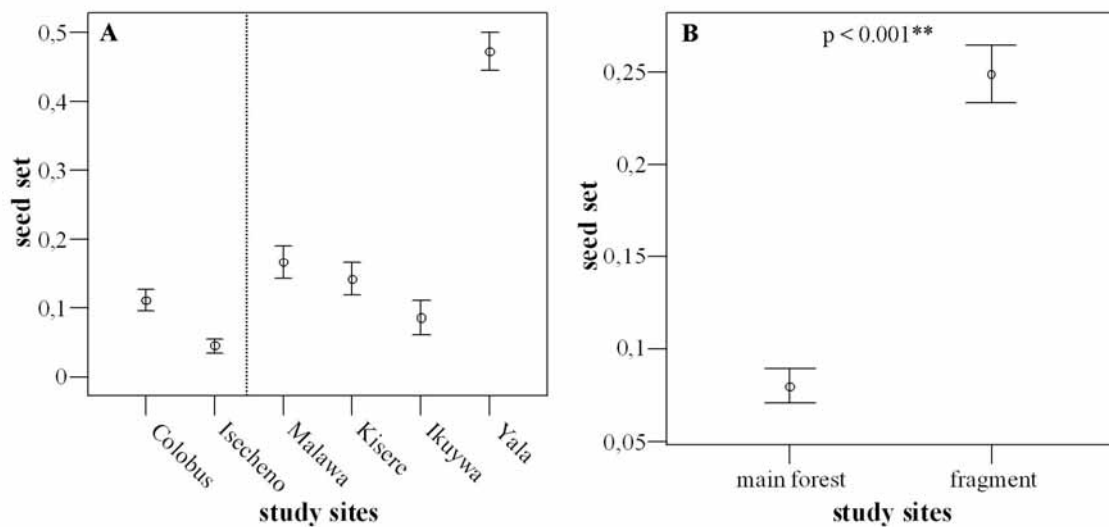


Fig. 47: Seed set of *D. fragrans* (error bars; standard error of mean value):
 (A) in two main forest (left of the dashed line) and three forest fragment (right of the dashed line) study sites arranged from north to south,
 (B) grouped in main forest (2) and forest fragment (3) study sites
 [tested for differences by one-way ANOVA]

The final model ($R^2=0.345$) of a backward multiple regression indicated the following group of factors which had a potential influence on the seed set of *D. fragrans* (Table 69): the percentage of forest in a buffer of 100m ($p=0.001^{**}$), a north-south gradient ($p=0.001^{**}$), the C/N ratio ($p=0.001^{**}$) and $[Mg^{++}]$ ($p=0.001^{**}$) of the soils and the protection status ($p < 0.001^{**}$).

A higher seed set of *D. fragrans* was found in study sites that were surrounded by a lower proportion of forest in a 100m buffer (range: 68% – 98%) and which were located further south. In addition, the seed set was higher in the less protected forest reserves and in soils with lower C/N ratio (range: 5 – 10) and lower $[Mg^{++}]$ (range: about 10 – 55 $mmol_c \cdot kg^{-1}$) (Fig. 48).

Table 69: Final model coefficients of a backward multiple regression (started with n=9 factors; Appendix 42)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	1.348	.080		16.954	.345	< .001**
% of forest in a 100m buffer	-.008	.001	-.334	-11.558		< .001**
North-south gradient	.040	.003	.256	14.262		< .001**
C/N ratio of the soil	-.045	.002	-.371	-18.295		< .001**
$[Mg^{++}]$ of the soil	-.015	.001	-.839	-25.903		< .001**
Protection status	.070	.011	.116	6.488		< .001**

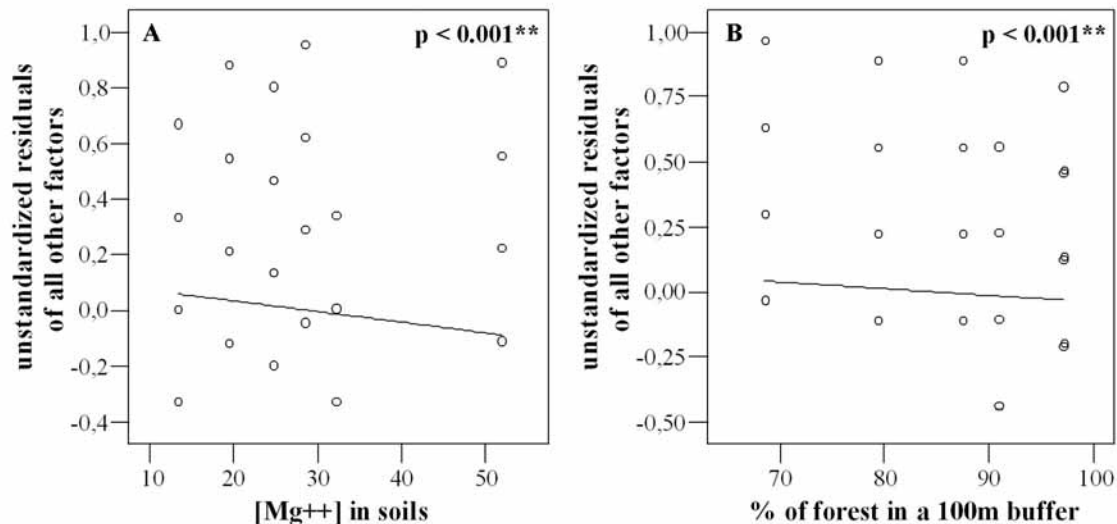


Fig. 48: Regression scatter plots *D. fragrans*: (dependent variable= seed set):
 (A) $[Mg^{++}]$ ($mmol_c \cdot kg^{-1}$) in soils to unstandardized residuals of all other factors
 (B) percentage of forest in a 100m buffer to unstandardized residuals of all other factors

These tendencies could not be shown in a multiple regression model on study site level with respect to the factors $[Mg^{++}]$ in soils and forest in a buffer of 100m (Table 70).

Table 70: Coefficients of a multiple regression (n=2 factors)

Factors	B	Standard error	Beta	t	R ²	Significance
(constant)	.916	.745		1.229	.553	.307
% of forest in a 100m buffer	-.005	.007	-.370	-.712		.528
$[Mg^{++}]$ of the soil	-.011	.006	-.939	-1.805		.169

6.4.5 Levels of pollination

Both the number of pollen on stigmas (Fig. 49A) and the fruit set (Fig. 49B) were higher in main forest study sites. In contrast to this, the seed set was significant higher in forest fragment plots (Fig. 49C).

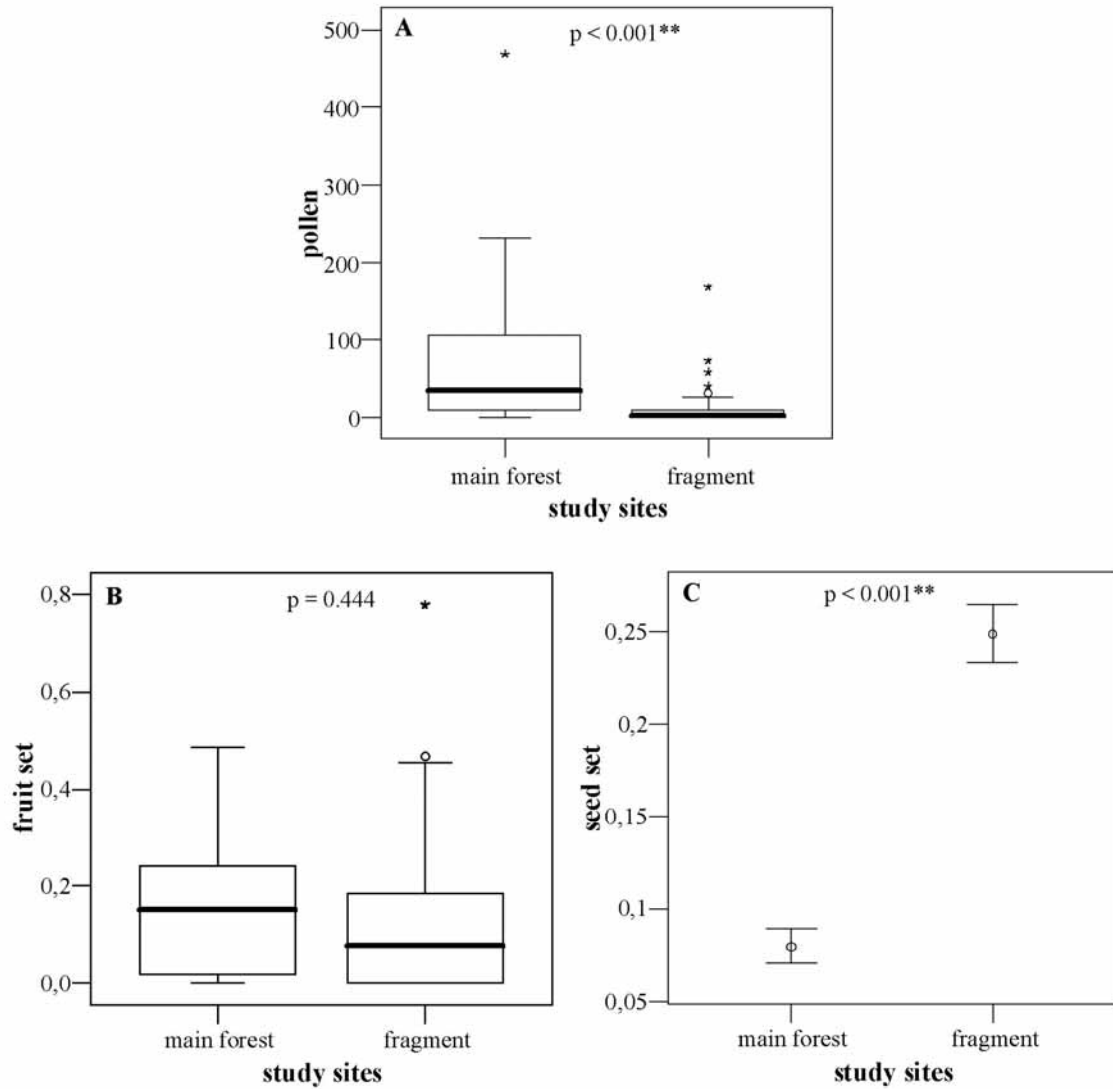


Fig. 49: Levels of pollination grouped in main forest and forest fragment study sites: (A) pollen on stigmas, (B) fruit set, (C) seed set (*Dracaena fragrans*)

7. Discussion

“*Gutiri keega kaumaga heega*” –
 “Nothing good comes out of an easy situation”
 (Kenyan saying)

In general, all field studies dealing with habitat fragmentation are afflicted with a huge number of influencing variables. This complexity of biotic and abiotic factors is making monocausal explanations pretty unlikely and predictions of specifics difficult or even impossible (Bissonette & Storch, 2002).

7.1 Visitation frequency and primary pollination success

Comparing all tested plant species of this study, a general tendency of a higher visitation frequency in forest fragment study sites was evident (Fig. 50), although different main pollinator groups were identified: honeybees (*Apis mellifera*) for *Acanthopale pubescens*; carpenter bees (genus *Xylocopa*) for *Acanthus eminens* or Halictids, Megachilids and a limited number of honeybees for *Heinsenia diervilleoides*. The collection of nectar was common factor for visitations for all observed bees.

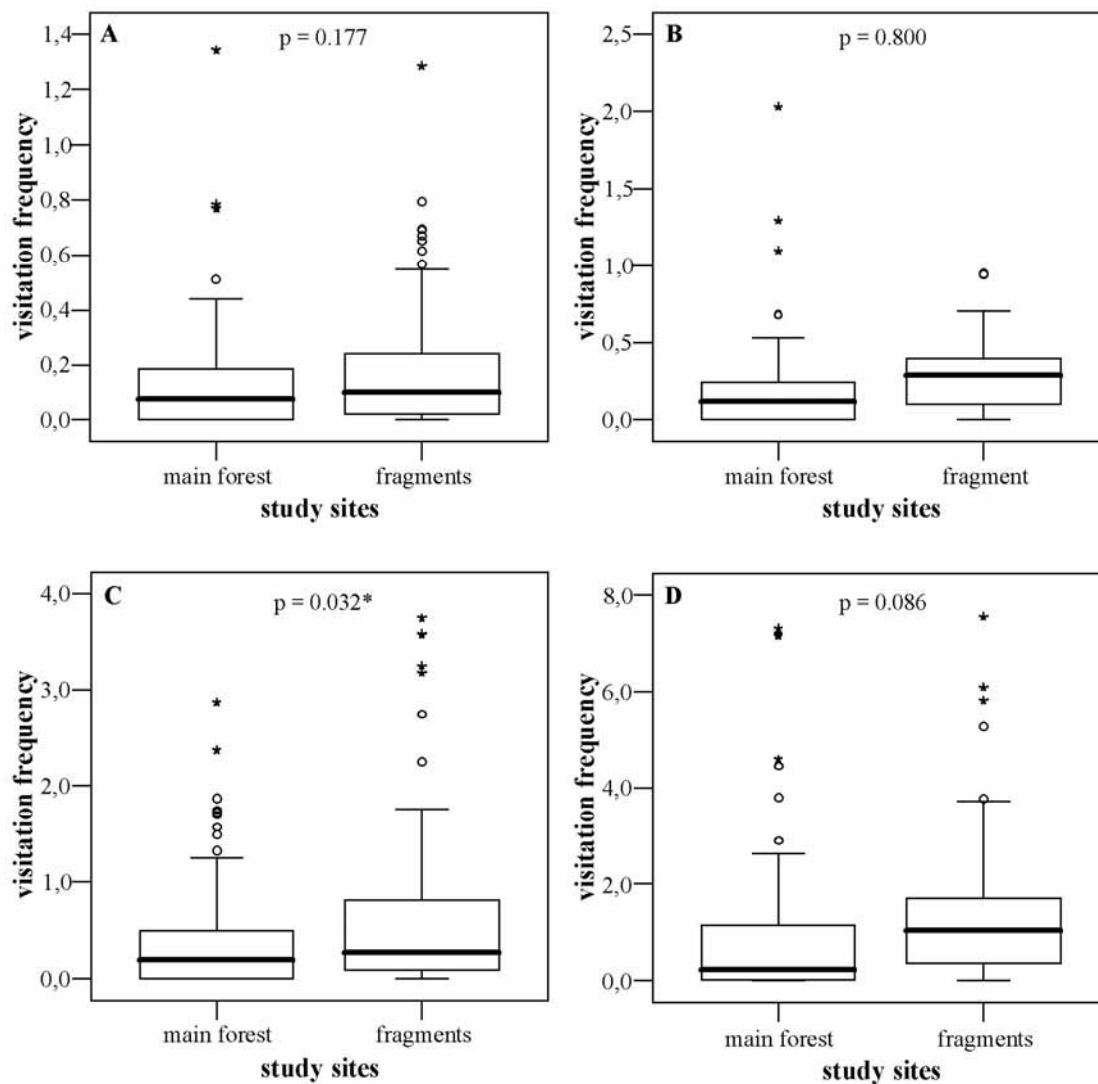


Fig. 50: Visitation frequency in study sites:
 (A) *Acanthopale pubescens*, (B) *Acanthus eminens* (campaign 2002),
 (C) *Acanthus eminens* (campaign 2003), (D) *Heinsenia diervilleoides*

The same phenomenon of a higher number of bird visits on tree flowers (*Embothrium coccineum* [Proteaceae]) in smaller (1 ha) compared to larger (>20 ha) rain forest fragments, has already been described from southern Chile (Smith-Ramirez & Armesto, 2003).

Higher visitation frequency is either the result of higher visitor abundance on the flowers or a higher number of visits per visitor. Both scenarios might be influenced by various abiotic and biotic factors: e.g. the microclimate like temperature, humidity and cloudiness; the diversity of habitat types; the diversity and abundance of plant and visitor species; the predation on visitors; the amount and quality of nectar, but also the availability of the resource nectar inside the forage range. At the same time many parameters are linked with each other.

Bee abundance

As generally known, bees invaded almost all parts of the world, nevertheless the greatest diversity is found in warm and dry areas (O' Toole & Raw, 1999). In addition, bees are more abundant in warm-temperate xeric regions (Michener, 1979). Along a humidity-gradient the greatest abundance of bees was also documented in the dryer extreme (Devoto et al., 2005). Here, nesting conditions might play an important role (Michener, 2000). However, other reasons for patterns of abundance of bees like diversity of habitat types (Steffan-Dewenter et al., 2002), plant diversity and abundance (Potts et al., 2001; Ghazoul, 2006) and predation of larvae by ants (Michener, 2000) have been reported. Two of these three factors also might promote higher abundance of bees inside the Kakamega Forest fragments as explained below.

The recently conducted bee study in and next to Kakamega Forest (Gikungu, 2006), showed a bee fauna richer in diversity and abundance around the forest compared to the forest islands itself. Generally a higher influence of the dryer bush and farmland and its bee populations could be postulated compared to the main forest, due to higher forest edge proportion of the forest fragments. As likely as not, foraging flights of these bees - many flights into the forest have been observed - might enclose the entire forest fragments (65 ha -1.370 ha). But in this context, Steffan-Dewenter et al. (2006) remarked that the response to habitat fragmentation on bee communities is still poorly understood.

Basically, the nectar gathered by foraging bees must cover the cost of collection and provide a surplus for personal and offspring need (Proctor et al., 1996). In tropical habitats, bee flight ranges have been studied in only a few species, but studies on *Apis mellifera* showed a peak foraging range of about 10 km and an average forage range between roughly 2 km and 5 km (Roubik, 1989). The same is true with the larger *Xylocopa* bees, where average forage ranges between 6 km and 10 km from the nest were documented (Roubik, 1989). Regarding the very tiny Halictids next to the forest, just a lower impact on the visitation frequency inside the forest sites could be expected, due to their general limited forage ranges of not more than about 1 km (Roubik, 1989). Nevertheless, because of the foraging efficiency, a pollen transfer between forest study sites appeared to be unlikely.

Given that the entire Kakamega Forest region was surrounded by a diverse farmland, especially around the forest fragments, a "higher diversity of habitat types" could also be postulated in relation to their sizes. This kind of more heterogeneous landscape is

expected to have higher abundances of wild bees on different scales (Steffan-Dewenter et al., 2002).

Even in Kakamega, a higher abundance of *Xylocopa calens* next to the forest, especially in the North (10 km transect) (Kasina, 2005), could be explained by a higher diversity of habitat types next to the forest. Furthermore the *Xylocopa* bees depend mainly on trees for nesting (M. Gikungu, pers. comm.). In contrast, the more homogeneous farmland in the South next to Kakamega Forest revealed no effects (Kasina, 2005). Concerning *A. pubescens* visited by honey bees, the same phenomenon could be observed, the visitation frequency was higher inside the northern compared to the southern study sites (Fig. 13B; Fig. 14B). Additionally, the local communities in the North housed more bees.

Becker et al. (1991) also reported in this context, that higher *Euglossa* bee abundance was found inside smaller forest fragments (up to 10 ha) in South America compared to larger forest fragments (100 ha) or the continuous rain forest. The authors also referred these effects to changes in the landscape matrix, which provides diverse nest sites.

The plant diversity (Althof, 2005) inside main forest or forest fragment sites showed no effects on the visitation frequencies or on the bee abundance. This could be explained due to nonexistent significant differences of species numbers, distributed in main forest sites (n= 103 to 163) or forest fragment sites (n= 93 to 138). The same was true, if main forest (middle-aged secondary) and forest fragment succession stages (heavily logged and planted, middle-aged secondary, old secondary, near-primary) were compared (Althof, 2005).

An additional explanation for a higher abundance of bees inside forest fragments appeared to be the predation of bee larvae by ants (Michener, 2000). Here, the abundance of the forest specialist army ant (genus *Dorylus*) showed a positive correlation to the forest size (Peters, 2003). Therefore lower predation pressure on bee larvae could be assumed inside the smaller forest fragments which potentially reflected bee abundance.

To all intents and purposes, studies of fragmentation and edge effects on pollinator populations should as well have temporal depth (Cane, 2001). In this context, Roubik (2001) showed ups and downs in pollinator populations over decades. This could be one possible explanation for the differences of the visitation frequencies inside the same study sites during the *A. eminens* campaigns 2002 and the campaign 2003.

Flower visitations

Apart from the postulated higher abundance of bees inside the forest fragments due to higher edge effect, several other biotic and abiotic factors might have influenced the visitation frequencies for the different observed plant species.

In general, *Acanthopale pubescens* appeared not to be very attractive to honey bees. Despite the fact that *A. pubescens* as a mass blooming plant species provided a great abundance of flowers, the overall visitation frequency of all study sites was very low with 0.16 visits/flower/hour. The visitation frequency even declined with a higher number of *A. pubescens* flower per observation unit (Table 14). This could mean that either the amount of nectar or the percentage of sugar in the nectar was very low, or both. But also the final multi regression model stressed the importance of the location of the study sites. Higher visitation frequencies became evident inside study sites where lesser forest was found in a buffer of 2000m around the study sites (Fig. 13A; Fig. 14A)

and which were located further north. These findings confirmed the assumption of a potential impact of the farmland bee populations with respect to the higher visitation frequencies of *A. pubescens* inside the forest fragments.

In contrast, the less abundant *Acanthus eminens* flowers were highly frequented by *Xylocopa* bees during both campaigns 2002: 0.282 visits/flower/hour and 2003: 0.52 visits/flower/hour. The negative correlation between visitation frequencies and cut trees per hectare during campaign 2002 (Fig. 24A) might lead to the suggestion that *Xylocopa* bees - as carpenter bees - lost potential nesting sites in higher disturbed forests. But also the more open canopy could have changed the nectar production due to higher solar radiation. Apart from this exogenic factor a strong genetic component on nectar production was reported (Kearns & Inouye, 1993).

Campaign 2003 showed a negative correlation of cloudiness and visitation frequency (Fig. 25). Here, the denser cloudiness could have influenced the foraging behaviour of the *Xylocopa* bees, the more clouds the less foraging flights. Furthermore, also with respect to the *A. eminens* campaign 2003 the final multi regression model stressed the importance of the location of the study sites; higher visitation frequencies were found in smaller forest fragments. As described for *Acanthopale pubescens*, these findings might confirm the assumption of a potential impact of the surrounding farmland bee populations on the forest visitation frequencies.

The differences between main forest and forest fragment visitation frequency in 2002 compared to 2003 should be traced back to lower study site samples or seasonal changes in the bee populations (Roubik, 2001).

Halictids and Megachilids as main pollinator groups of *Heinsenias diervilleoides*, nest in exposed areas of the forest, especially in disturbed sites and along forest pathways, but also outside the forest (M. Gikungu, pers. comm.). In particular for Halictids, combined with their limited forage ranges, a higher visitation frequency should be an indicator for a higher abundance of bees. Here, the positive correlation between the amount of cut trees per hectare and the visitation frequencies inside the study sites supported this assumption (Fig. 36A; Fig. 37A).

In Kakamega Forest the oldest succession stages were found in the fragments Kisere and Yala compared to the middle-aged secondary study sites in the main forest (Althof, 2005). Consequently, the higher visitation frequencies on *H. diervilleoides* flowers in older succession stages of the forests (in particular in Kisere and Yala) (Fig. 36B; Fig. 37B) could result from lower predation pressure on bee larvae by army ants (genus *Dorylus*) inside the smaller forest fragments (Peters, 2003) which potentially reflected positively on the bee abundance.

A closer examination of the visitation frequency data showed also differences on spatial scales. Here, high variations were found on study site as well as on observation unit data level. One likely explanation to this could be a possible dependency of bee foraging behaviour with respect to microhabitat factors, as for example, the different macroclimate or varieties in the blooming composition. But also special foraging strategies, such as group-foraging of non-social bees as described by Proctor et al. (1996), might inherently provoke disproportionate shifts concerning mean study site visitation frequencies of, for instance, the *H. diervilleoides* campaign.

In this context, Steffan-Dewenter et al. (2006) stressed that the variation of plant-pollinator interactions in response to habitat fragmentation on the spatial and temporal scales is still less understood.

Flower visitations and pollen transfer

All observed plant species in this study were found inside Kakamega Forest and its fragments. Due to the long distances between these forest remnants and the highly attractive composition of flowering plants in the bush- and farmland in between, it can be postulated that no intensive exchange of genetic material through pollination occurred between these forest fragments.

In addition, this study showed at the forest fragment level that high visitation frequencies do not inevitably lead to more pollen on stigmas. Only *A. eminens* (campaign 2003) showed a positive correlation between visitation frequencies and counted pollen on stigmas (Fig. 34). Here, higher visitation frequency in forest fragments might lead to more pollen on stigmas. Hence, a potential pollinator and/or pollen limitation could be assumed on *A. eminens* flowers in 2003, in particular due to the fact that 34.7% of the forest fragment and even 55.8% of the main forest stigmas did not show any deposited pollen grain.

In contrast to this, with respect to *A. pubescens*, *A. eminens* (campaign 2003) and *H. diervilleoides* a contrary relation between visitation frequency and number of pollen on stigmas became obvious.

Generally, it has to be considered that each visitor was potentially able to transfer either a large number or even no pollen grains with every visit. But a higher number of visitors might also have removed a higher number of pollen grains from the stigmas.

Pollen on stigmas

In this study, no general pattern of higher or lower amounts of pollen in main forest or forest fragment study sites were evident (Fig. 51).

On closer examination, a very high variability of pollen number on stigmas was evident with respect to all observed plant species. The standard deviation in many cases was even higher than the counted mean number of pollen on stigma. Therefore, interpretations concerning the potential influences of the measured biotic and abiotic factors should be of limited significance. In addition, the final models of multiple regressions also showed either a larger quantity of potential influencing variables and/or only a low explanatory power (R^2).

In general, differences of pollen numbers on stigmas might be rather a result of biotic effects – such as the transfer by pollinators, plant species specific reasons and/or genetic variations in the populations - than due to discrepancies of the abiotic factors.

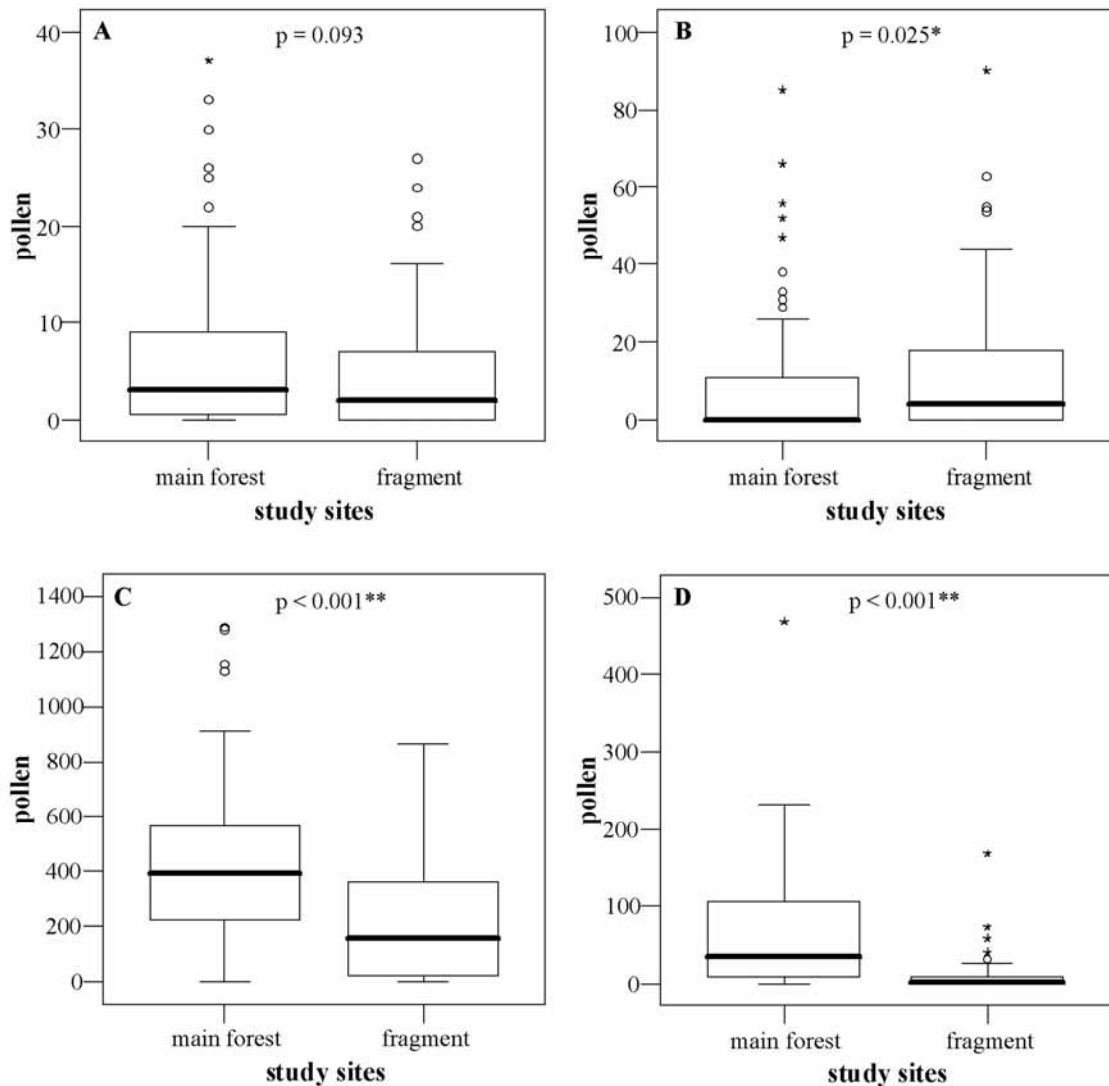


Fig. 51: Pollen on stigmas in study sites:
 (A) *Acanthopale pubescens*, (B) *Acanthus eminens* (campaign 2003),
 (C) *Heinsenia diervilleoides*, (D) *Dracaena fragrans*

7.2 Reproductive success

In this study reproductive success was defined as fruit times seed set. More extensive studies should also take the ability of germination and seedling establishment into consideration.

Fruit set

With respect to the four observed plant species, no general pattern of higher or lower fruit set in main forest or forest fragment study sites was evident (Fig. 52). Just *A. pubescens* and *H. diervilleoides* showed highly significant differences between fruit set in main forest and fragment forest study sites. Particularly, lower fruit set was found in *A. pubescens* forest fragment plots and with regards to *H. diervilleoides* inside main forest sites.

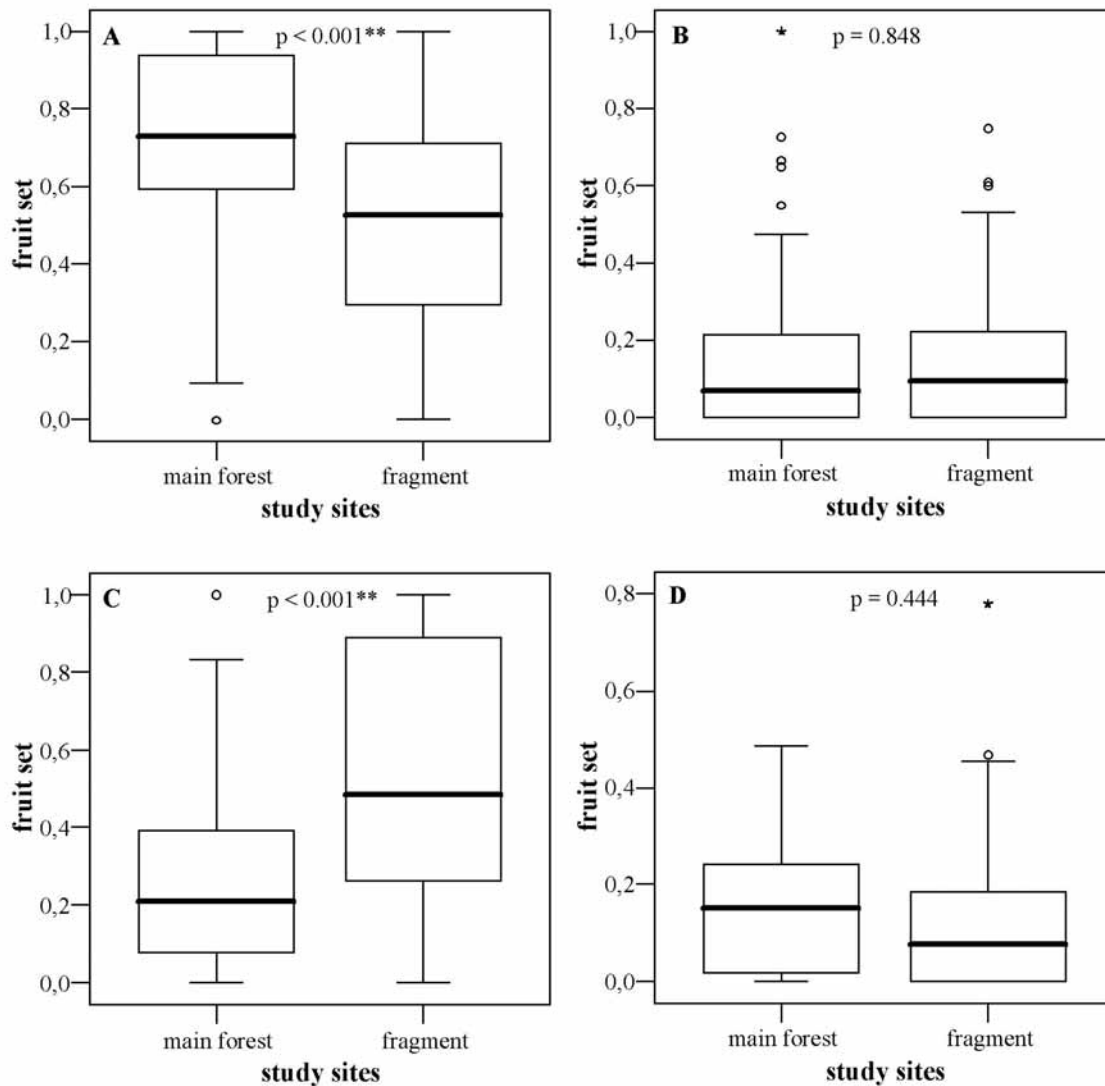


Fig. 52: Fruit set in study sites:

(A) *Acanthopale pubescens*, (B) *Acanthus eminens* (campaign 2003),
(C) *Heinsenias diervilleoides*, (D) *Dracaena fragrans*

This inconsistent response of fruit set with respect to different plant species was also reported in other empirical studies. Here, both a decrease (Oostermeijer et al., 1992; Groom, 1998; Wolf et al., 1999) and an increase (Aizen & Feinsinger, 1994a; Cunningham, 2000b) of fruit set in fragments relative to continuous habitats were described. Changes in the abiotic environment caused by fragmentation (Harris, 1988; Laurance & Yensen, 1991; Saunders et al., 1991; Murcia, 1995), but also changes in the animal communities of fragments (Cunningham, 2000b) appeared to be the main influencing factors.

In this study, personal observations of a lot more feeding damages on *A. pubescens* fruits in forest fragments might stress the importance of herbivores as one main influencing factor of fruit set. Here, also a significant lower fruit set in smaller forest fragment study sites (Fig. 18) could be explained by a possibly higher abundance of herbivores inside smaller fragments. In this context, theoretical and empirical studies have shown that longevity and frequency of herbivore outbreaks were positively correlated with the degree of fragmentation (Kareiva, 1987; Roland, 1993; Rothman &

Roland, 1998; Kondoh, 2003). Freund (2004) also described seasonal varieties in the abundance of herbivores inside the differed Kakamega Forest fragments. (Freund, 2004)

With respect to *A. eminens* (campaign 2003); many fruits were found in various stages of rot inside all study sites. Thus, a negative dependency to moisture connected with solar radiation could be assumed regarding *A. eminens* fruit set. This assumption might be consolidated, because of higher fruit set in study sites which were less protected and located nearer to the forest edges (Fig. 29; Fig. 30).

In this study no factors became evident which could explain substantially the significant lower fruit set of *H. diervilleoides* inside main forest study sites. But among others, the correlations between fruit set and a north-south gradient allowed assumptions that different soil types and parameters might influence the fruit synthesis of *H. diervilleoides*. The fruit set of *D. fragrans* showed no response to all observed factors.

Subsumed, fruit set might mainly be resource limited, but not pollinator limited, and therefore changes in pollinator abundance would be less important (Schemske & Horvitz, 1988).

Seed set

Seed production could not easily be linked to habitat fragmentation, but fragmentation might affect plant population genetics by loss of alleles through drift and by inbreeding (Ghazoul & McLeish, 2001; Ghazoul, 2005). Several studies reported that small plant populations in fragmented habitats showed reduced seed set, genetic diversity and offspring fitness (Oostermeijer et al., 1994; Fischer & Matthies, 1997; Fischer & Stöcklin, 1997; Morgan, 1999; Hendrix & Kyhl, 2000; Kéry et al., 2000; Luijten et al., 2000). In this context, Steffan-Dewenter et al. (2006) remarked that relatively few studies included direct observations of flower visitation and experimentally test for pollinator limitation as the cause for lower seed set. But also different studies were published, which showed non-significant or significant positive effects of fragmentation or isolation on reproductive success (Spears, 1987; Aizen & Feinsinger, 1994a; Aldrich & Hamrick, 1998; Cunningham, 2000b; Costin et al., 2001).

All in all, the tested plant species of this study showed a general tendency for higher seed set in forest fragment study sites (Fig. 53), *H. diervilleoides* and *D. fragrans* even a highly significant tendency.

In general, seed set is mainly depending on either pollen quantity and/or pollen quality (Waser & Price, 1991; Ramsey & Vaughton, 2000). Several factors have been described which might contribute to insufficient pollination (Waser & Price, 1991; Brown & Kephart, 1999), such as low visitation frequencies or poor genetic variation inside the plant population gene pool.

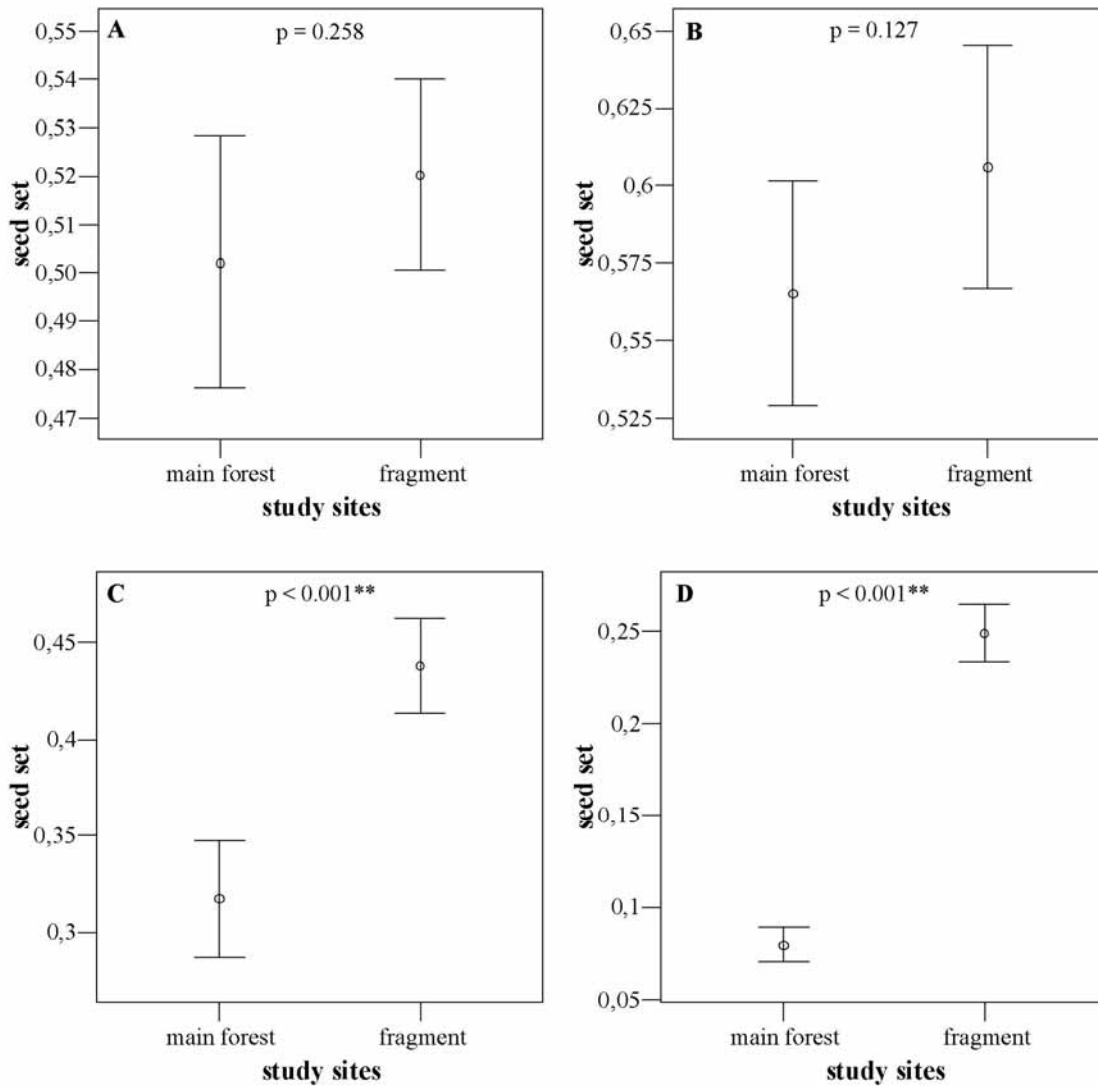


Fig. 53: Seed set in study sites:

(A) *Acanthopale pubescens*, (B) *Acanthus eminens* (campaign 2003),
(C) *Heinsenya diervilleoides*, (D) *Dracaena fragrans*

A number of studies reported that pollen limitation (pollen quantity) is a common proximate cause of low seed set (Burd, 1994; Ramsey & Vaughton, 2000). Here, with the exception of the *A. eminens* campaign 2003, no pollen limitation on forest fragment level could be assumed due to the non-correspondence of the pollen number on stigmas and seed set (Fig. 21, Fig. 33, Fig. 34, Fig. 42, Fig. 49).

Therefore, the pollen quality at the forest fragment level might be one main reason for lower seed set inside the main forest. In this context, poorer pollen quality could mean self or incompatible pollen and closely related pollen (Manasse & Pinney, 1991; Waser & Price, 1991; Byers, 1995; Totland et al., 1998).

In general, the self-pollination experiments of this study indicated a need for cross-pollination to all observed plant species. *A. pubescens*, *A. eminens* and *D. fragrans* showed ability for autogamy, but these seeds looked poorer and smaller than regular pollinated ones. *H. diervilleoides* even produced no fruits in self-pollination experiments.

For this reason, higher seed set in forest fragment sites might be a consequence of higher genetic variation (Olesen & Jain, 1994; Oostermeijer et al., 1994). This

assumption at first looked implausible, but closer examination of the Kakamega Forest fragmentation history, suggest that the results of the visitation frequencies and the patchy plant distribution could support this hypothesis.

First of all, due to the very young forest fragments (about 100 years or younger), the plant populations inside these fragments should have more or less the same genetic variation as those in the main forest. In addition, the sizes of the forest fragments are still rather large (65-1,370 ha), compared to the main forest (8,245 ha).

However, another crucial factor appeared in this study; there is also a generally higher visitation frequency inside the forest fragment study sites. With the aforementioned exception of the *A. eminens* campaign 2003, this higher visitation frequencies were not leading to a higher amount of pollen on stigma, but could have led to higher genetic intermixture through higher rates of long-distance cross-pollination events (Schmitt, 1983). In addition, the postulated higher pollinator abundance inside the forest fragments also could cause higher foraging ranges, because of the higher number of competitors.

Consequently, the patchy distributed plant populations inside the forest fragments could have been better connected through pollination, resulting in higher genetic variation in these populations and in consequence a higher seed set. In this context, Montgomery et al. (2003) were able to show that the boost of seed set of *Peraxilla tetrapetala* (Loranthaceae) on forest edges was directly linked to a higher number of visits by the pollinating birds.

In the long run, in contrast, genetic erosion appears more likely in plant populations located in forest fragments, because of the lower number of plant individuals distributed in smaller forest areas. This was shown already in isolated populations of a neotropical rain forest canopy tree (*Pithecellobium elegans* [Mimosaceae]) (Hall et al., 1996). In addition, undergoing population decline and fragmentation of many plant species in the tropics is making Allee effects on seed production likely to become increasingly relevant to plant species conservation (Ghazoul, 2005).

In this study, *A. pubescens* showed a rather low number of flower visitations but also a tendency of higher visitation frequencies and seed set inside fragment study sites. These results might support the hypothesis of a temporarily higher genetic variation inside forest fragment populations. In addition, higher seed set was found in forests sites where a higher number of paths (n=0–20) were counted (Fig. 20). Due to the biology of *A. pubescens* as a disturbance indicator (E. Fischer, pers. comm.), these findings also could document a more intensive exchange of genetic material through pollination, because of better connection of the patchy distributed plant population through populations along the paths.

The *Acanthus eminens* campaign 2003 showed very low mean pollen numbers on stigmas inside the study sites (5.09 to 11.96), a high percentage of completely unloaded stigmas (34.2 %) and a higher amount of pollen on stigmas in forest fragment sites (Fig. 27D). The seed set also was higher (Fig. 31). These observation results allowed the assumption that seed set was strongly limited by pollen quantity. In addition, seed set was higher in study sites which were surrounded by a higher percentage of forest in a buffer of 100m (Fig. 32). This finding corresponded with the results of the pollination biology study conducted by Dietzsch (2004) focusing on *Acanthus eminens* (forest confined) and *Acanthus pubescens* (open grassland confined); Dietzsch showed that heterospecific pollen has the potential to reduce seed set of both related species.

In addition to this possible pollen limitation, pollen quality might also have had a strong impact on seed set. As described for *A. pubescens*, *A. eminens* (campaign 2002 and

2003) also showed higher visitation frequencies and higher seed sets in the forest fragments (Fig. 33; Fig. 34).

A high percentage of closely related pollen on stigmas of *H. diervilleoides* could be assumed in general, given that the main pollinator groups such as the tiny Halictids and Megachilids show a very restricted foraging range. In addition, the higher number of pollen on stigmas found in main forest study sites might lead to lower seed set (Fig. 42), if stigma clogging occurred or numerous pollen tubes either exhausted styler resources or diverted entry into ovules (Lloyd & Yates, 1982; Snow, 1986; Bertin, 1990). All other tested abiotic and biotic factors showed only weak evidences for influencing the seed set of *H. diervilleoides*. In contrast to this, higher visitation frequencies found in forest fragments, again allowed the assumption of a higher rate of cross-pollination events in here, which might have led to higher seed set in these populations.

The same could be the case regarding *D. fragrans*, where significant higher seed set inside the forest fragment study sites occurred, despite significantly lower number of pollen on the stigmas at these sites.

Furthermore, an inverse correlation of soil nutrient concentration on seed set, in this study, characterized by the exchangeable bases Magnesium (Mg^{++}), was evident (Fig. 48). This effect appeared beyond the deficient level of $[Mg^{++}]$ in soils of less than $10 \text{ mmol}_c \cdot \text{kg}^{-1}$ (Musila et al., 2005), between 10 to $60 \text{ mmol}_c \cdot \text{kg}^{-1}$, and could consequently describe a toxic $[Mg^{++}]$ gradient to *D. fragrans*. In this context, a potentially toxic effect of very high $[Mg^{++}]$ was reported, whereby potassium absorption was impeded (Sitte et al., 1991). But this inverse correlation also could have occurred as a statistical artifact, because of the factor of forest in a buffer of 100m the significance of this correlation disappeared at the study site level.

Finally, Steffan-Dewenter et al. (2006) suggested to perform pollination experiments to assess the maximum seed set after cross-pollination for a better understanding of pollination failure due to habitat fragmentation.

Fruit and seed set

With the exception of *A. pubescens* reproductive success, defined as a product of fruit and seed set, showed the same tendency as mean seed set with higher values inside forest fragments compared to the main forest (Table 71). Here, the higher reproductive success of *A. pubescens* in the main forest resulted from a highly significant higher fruit set, which could be attributed to higher *A. pubescens* specific herbivore abundance inside the forest fragments.

Table 71: Levels of pollination (in red the higher values)

<u>Plant species</u>	<u>Main forest sites:</u> visitation frequency/ pollen on stigmas/ reproductive success	<u>Forest fragment sites:</u> visitation frequency/ pollen on stigmas/ reproductive success
<i>A. pubescens</i>	0.14/ 6.58 / 0.36	0.17 / 4.46/ 0.27
<i>A. eminens</i> '02	0.27/ 4.24 / 0.04	0.29 / 1.59/ 0.17
<i>A. eminens</i> '03	0.41/ 7.29/ 0.08	0.67 / 10.72 / 0.09
<i>H. diervilleoides</i>	0.94/ 409.06 / 0.08	1.38 / 221.97/ 0.24
<i>D. fragrans</i>	--/ 67.76 / 0.01	--/ 10.23/ 0.03

As mentioned above, a possible higher genetic variation inside the plant populations might be one reason for this general higher reproductive success inside the forest fragments of Kakamega Forest. Ghazoul (2005) remarked that all studies which recorded negative effects on plant fecundity due to population sizes, described plant individual numbers in populations with less than 50. With possible exceptions of *H. diervilleoides* populations, all other observed forest fragment plant populations in this study still contained higher individual numbers.

7.3 Plant species and fragmentation

Cane (2001) emphasised that several authors concluded that habitat fragmentation is broadly deleterious, but their own data showed that some native species proliferate in fragments.

This thesis showed, partly significant, but not unanimous differences at various levels of pollination, if main forest and forest fragment study sites were compared (Table 72). Consequently, an immediate and/or indirect effect of forest fragmentation on the observed plant species could be assumed.

Table 72: Differences in forest fragment compared to main forest study sites (↓ = higher; ↑ = lower)

<u>Plant species</u>	Visitation frequency	Pollen on stigmas	Fruit set	Seed set	Reproductive success
<i>A. pubescens</i>	↑ (p=0.177)	↓ (p=0.093)	↓ (p<0.001**)	↑ (p=0.258)	↓
<i>A. eminens</i> '02	↑ (p=0.800)	↓ (p=0.006**)	↑ (p<0.001**)	↑ (p=0.143)	↑
<i>A. eminens</i> '03	↑ (p=0.032*)	↑ (p=0.025*)	↑ (p=0.848)	↑ (p=0.127)	↑
<i>H. diervilleoides</i>	↑ (p=0.086)	↓ (p<0.001**)	↑ (p<0.001**)	↑ (p<0.001**)	↑
<i>D. fragrans</i>	-	↓ (p<0.001**)	↓ (p=0.444)	↑ (p<0.001**)	↑

Aizen et al. (2002) reviewed 25 studies (1987–2001) assessing the effects of habitat fragmentation on either pollination or reproductive success of 46 plant species in different types of habitat. In the end, they suggested that no generalizations can be made of how plant reproduction responds to habitat fragmentation as both significantly negative and significantly positive effects of fragmentation were found besides non-significant effects on pollination and reproductive success. The same appeared to be true for this study in the Kakamega rain forest. As a conclusion Aizen et al. (2002) remarked that it is unlikely that one or a few traits and/or ecological processes will be enough to explain why pollination and reproduction decline with fragmentation in many species but not in others.

In general, a number of factors have to be considered for reasonable comparisons of fragmentation studies.

One crucial variable appeared to be the size of included fragments. Ghazoul et al. (2001), for example, conducted a fragmentation study in dry deciduous forests in Costa Rica and reported both reduced fertilisation and seed set in smaller fragments regarding the tree species *Anacardium excelsum* [Anacardiaceae]. Just by the fragment sizes in his study (in the main between 0.3 and 48 ha) a transfer, or even a generalisation of its findings appeared to be very problematic to other forest systems, such as Kakamega Forest (fragment sizes between 65 to 8.245 ha). In addition, Morgan (1999) stressed that also the history of the fragmentation process in studies has to be considered.

Another important parameter is how the visitation frequencies data were collected. Here, short distance observations (like practised in this study), the use of video cameras (Cunningham, 2000a) or less precise methods, like binocular inspections of tree canopies (Ghazoul & McLeish, 2001), have been described.

But also the individual biology of each plant species might play a crucial role. The Acanthaceas *A. pubescens* and *A. eminens* in this study for instance, as disturbance indicators (E. Fischer, pers. comm.), prefer paths or forest gaps. Due to this distinct ecological niche the populations of these plant species were even fragmented inside the main forest. But, with regards to their restricted seed dispersal opportunity, owing to the fruit type of capsules, genetic exchange mainly occurs through pollination. Hence, the higher visitation frequencies in forest fragments could lead to higher reproduction success.

The same effect could be assumed concerning the very scattered distribution of flowering *H. diervilleoides* individuals: the higher visitation frequencies in forest fragments did not consequently lead to a higher number of pollen on stigmas. However, through a generally higher number of flower visits by pollinators inside the forest fragments the likelihood of long-distance cross-pollination might increase.

A lack of information concerning the pollinators and the visitation frequencies of *D. fragrans* complicated the interpretation of the higher number of pollen on stigmas in the main forest, and higher seed set in the forest fragments. Here, the widespread distribution inside the Kakamega Forest remnants (Althof, 2005) and the potential of vegetative reproduction through rhizomes led to the suggestion that the pollen found on *D. fragrans* stigmas might be closely related. But also in this study, in addition to possibly greater intensive exchange of genetic material through higher visitation rates of moths (see 6.4.1 covering experiment), a higher number of frugivores inside the Kakamega Forest fragments (Farwig, 2005) - birds that also should feed on the reddish *D. fragrans* fruits - might lead to higher seed set inside the forest fragments.

Finally, in case of further degradation and fragmentation of the Kakamega Forest remnants and its plant populations, combined with longer periods of isolation, an increased inbreeding could lead in the long-term to a decrease of individual fitness which might enhance the risk of population extinction. But only if the Kakamega Forest will exist that long?!

8. Outlook

The results of this thesis pointed to the fact that the genetic variation in the plant populations of the Kakamega Forest and its fragments might present a crucial parameter relating to the reproductive success of the different plant species. For a better understanding of these complex coherences further population genetic studies at the forest study site level could be very valuable.

In addition, the heterogeneous findings with respect to the different plant species, showed the necessity of a greater extent of plant-pollinator interaction studies in rain forests on the one hand, and the implication of other plant regeneration processes like seed dispersal and seedling establishment on the other hand. In this context, Harris et al. (2004) suggested in a review article dealing with the consequences of habitat fragmentation for plant-pollinator mutualism, that studies of whole suites of species will always be more informative than studies of single species that have prevailed until now. But also the importance of the agricultural landscape imbedded rain forests, as nutrition and nesting resource for forest plant and crop pollinators, should be studied in more detail.

The pushing requests by policy makers for obtaining consolidated recommendations for a sustainable use of forests and its biodiversity, particularly, stresses the demands of a better understanding of the underlying ecosystem services. But in this study the generalisation of habitat fragmentation effects for land-use planning and conservation appeared to be rather difficult. Dillard (2002) assigned three reasons for this: (1) the high specificity of the taxa, spatial scales, and ecological processes; (2) the variation according to the landscape types and its structure; and (3) the dominance of local effects, such as changes to certain microhabitat features.

Nevertheless, even economic advisors to governments (Sachs, 2005), realised that the loss of “*natural capital*”, described as ecosystems and their biodiversity, will have serious adverse consequences for the whole society or even the whole planet. Therefore, requirements that governments have a crucial role to play in conserving natural capital, have to be supplemented with the suggestions of Leakey (2002). He emphasized that especially poor countries like Kenya, which almost declared one-fourth of their land area as biological reserves, need and deserve financial support from the richer countries. In this context, Leakey (2002) also highlighted the concepts of protected National Parks and eco tourism. The new Forests Bill in Kenya (2005), in which a participatory forest management is aimed, might also contain chances for an existence of the Kakamega Forest over a longer period.

9. Summary

Rain forest fragmentation can affect plant-pollinator interactions and the reproductive success of plant species. Understanding these consequences is a crucial component of conserving vulnerable ecosystems.

In this study, conducted between June 2001 and March 2003 in the highly fragmented Kakamega Forest and its five larger forest fragments in Western Kenya, four plant species: *Acanthopale pubescens* [Acanthaceae] (June 2001 to December 2001), *Acanthus eminens* [Acanthaceae] (January 2002 to March 2002 and November 2002 to February 2003), *Heinsenia diervilleoides* [Rubiaceae] (November 2002 to March 2003) and *Dracaena fragrans* [Ruscaceae] (July 2002 to March 2003) were tested for the effect of forest fragmentation on visitation frequency, primary pollination success, fruit and seed set. Furthermore, several biotic and abiotic factors, such as plant species diversity, the succession stages of the study sites, the number of cut trees per hectare, the protection status and parameters of climate and soil, were related to these different levels of pollination.

In general, a higher mean visitation frequency and mean seed set was found inside the surrounding forest fragments compared to the main forest. In contrast to this, the primary pollination success and fruit set varied with respect to the different plant species.

Only regarding the *A. eminens* campaign 2003, the higher number of visits by the pollinating *Xylocopa* bees inside the forest fragments, consequently caused a higher number of pollen on stigmas and increased fruit and seed set. Thus, a pollinator and/or pollen limitation in the patchy distributed *A. eminens* population might have occurred in 2003. Due to the generally lower primary pollination success inside the forest fragment populations of all other plant species, one essential factor of the higher seed set might be an increase of the long-distance cross-pollination ratio owing to the higher visitation frequency, shown for *A. pubescens* and *H. diervilleoides*. Even a temporarily higher genetic variation could be postulated.

Nevertheless, for longer periods a reduction in population size and an increase in isolation due to fragmentation may lead to limited gene flow, increased inbreeding, loss of genetic variation, decreased individual fitness, and consequently to an increased risk of population extinction.

These complex coherences combined with several other possible influencing factors and the heterogeneous findings on plant species level, also on spatial and temporal scales, emphasized the need of further pollination studies in fragmented rain forests, particularly with regard to the demands by policy makers for receiving consolidated recommendations for a sustainable use of forests and its biodiversity.

Zusammenfassung

Die anthropogen bedingte Fragmentierung von tropischen Regenwäldern kann sich sowohl auf Tier-Pflanzen-Interaktionen als auch auf den Reproduktionserfolg von Pflanzen auswirken. Die Aufklärung dieser komplexen Zusammenhänge ist eine bedeutende Komponente zum möglichen Schutz wertvoller Ökosysteme.

In dieser zwischen Juni 2001 und März 2003 im Kakamega Forest, einem fragmentierten Regenwald und seinen fünf größeren Waldfragmenten im Westen Kenias durchgeführten Studie, wurden Besuchsfrequenzen, primärer Bestäubungserfolg sowie Frucht- und Samenansätze folgender Pflanzenarten auf mögliche Effekte der Waldfragmentierung untersucht: *Acanthopale pubescens* [Acanthaceae] (Juni 2001 bis Dezember 2001), *Acanthus eminens* [Acanthaceae] (Januar 2002 bis März 2002 und November 2002 bis Februar 2003), *Heinsenia diervilleoides* [Rubiaceae] (November 2002 bis März 2003) und *Dracaena fragrans* [Ruscaceae] (Juli 2002 bis März 2003). Des Weiteren wurde der mögliche Einfluss diverser biotischer und abiotischer Faktoren wie z.B. Diversität der Pflanzen, Sukzessionsstadien der Untersuchungsgebiete, Anzahl gefällter Bäume pro Hektar, Schutzstatus, klimatische Einflussgrößen und Bodenparameter, auf die oben genannten Ebenen der Bestäubung getestet.

Im Vergleich zum Hauptwald konnten in den umliegenden Waldfragmenten bei allen Pflanzenarten höhere Besucherfrequenzen und Samenansätze festgestellt werden. Dagegen ergab sich beim Vergleich des primären Bestäubungserfolges und des Fruchtansatzes kein einheitliches Bild.

Entgegen vorheriger Annahmen ergab nur die Untersuchung von *A. eminens* im Jahre 2003, dass eine höhere Besucherfrequenz der bestäubenden *Xylocopa*-Bienen zu einem größeren primären Bestäubungserfolg und einem höheren Frucht- und Samenansatz in den Waldfragmenten führte. Dieses Ergebnis lässt die Vermutung zu, dass nur die *A. eminens* Populationen im Jahre 2003 einer Bestäuber- und/oder einer Pollenlimitierung unterlagen. Bei der Untersuchung der anderen Pflanzenarten zeigte sich, dass eine höhere Besuchsfrequenz nicht zu einem größeren primären Bestäubungserfolg führte. Eine mögliche Erklärung für den trotzdem höheren Samenansatz könnte hier eine höhere Fremdbestäubungsrate, verursacht durch die höhere Besuchsfrequenz, sein. Auch eine temporäre Erhöhung der genetischen Variation innerhalb der inselhaft verbreiteten Pflanzenpopulationen wäre dadurch denkbar.

Auf lange Sicht dagegen könnte eine Reduktion der Populationsgrößen und eine steigende Isolation durch Fragmentierung zu einem verminderten Genfluss, einer steigenden Inzucht, einem Verlust an genetischer Variabilität, einer abnehmenden biologischen Fitness und somit zu einem ansteigenden Risiko des Aussterbens führen.

Diese komplexen Zusammenhänge, kombiniert mit einer Vielzahl anderer möglicher Einflussgrößen und der heterogenen Ergebnisse der verschiedenen Pflanzenarten, bekräftigen den Bedarf für weitere Bestäubungsstudien in fragmentierten Regenwäldern. Ebenso erfordern die drängenden Anfragen von Entscheidungsträgern, die Handlungsempfehlungen für eine nachhaltige Nutzung der Wälder und ihrer Biodiversität erwarten, weiterführende Studien auf diesem Gebiet.

10. References

- AGNEW, A. D. & AGNEW, S. (1994). *Upland Kenya Wild Flowers*. East African Natural History Society, Nairobi.
- AGREN, J. (1996). Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* **77**, 1779-1790.
- AIZEN, M. A., ASHWORTH, L. & GALETTO, L. (2002). Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science* **13**, 885-892.
- AIZEN, M. A. & FEINSINGER, P. (1994a). Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* **75**, 330 - 351.
- AIZEN, M. A. & FEINSINGER, P. (1994b). Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine Chaco Serrano. *Ecological Applications* **4**, 378 - 392.
- ALDRICH, P. P. & HAMRICK, J. L. (1998). Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* **281**, 103-105.
- ALTHOF, A. (2005). Human Impact on Flora and Vegetation of Kakamega Forest, Kenya. PhD thesis, Universität Koblenz-Landau.
- API. (2003). *Plan of Action of the African Pollinator Initiative*. African Pollinator Initiative Secretariat, Nairobi.
- BACKHAUS, K., ERICHSON, B., PLINKE, W. & WEIBER, R. (2003). *Multivariate Analysemethoden*, 9th edition. Springer-Verlag, Berlin & Heidelberg.
- BATES, H. W. (1864). *The Naturalist on the River Amazons*, 1962 edition. University of California Press, Berkeley.
- BECKER, P., MOURE, J. S. & PERALTA, F. J. A. (1991). More about euglossine bees in Amazonian forest fragments. *Biotropica* **23**, 586-591.
- BEENTJE, H. J. (1994). *Kenya Trees, Shrubs and Lianas*. National Museums of Kenya, Nairobi.
- BENNUN, L. & NJOROGE, P. (1999). Important Bird Areas in Kenya. The East Africa Natural History Society, Nairobi, Kenya.
- BERTIN, R. (1990). Effects of pollination intensity in *Campsis radicans*. *American Journal of Botany* **77**.
- BISSONETTE, J. A. & STORCH, I. (2002). Fragmentation: is the message clear? *Conservation Ecology* **6**, 14 [online] URL: <http://www.consecol.org/vol6/iss2/art14>.
- BLACKETT, H. L. (1994). Forest inventory report No. 3: Kakamega (KIFCON). National Museums of Kenya, Nairobi.
- BLEHER, B., USTER, D. & BERGSDORF, T. (2005). Assessment of threat status and management effectiveness in Kakamega Forest, Kenya. *Biodiversity and Conservation*.
- BROOKS, T. M., PIMM, S. L. & OYUGI, J. O. (1999). Time Lag between Deforestation and Bird Extinction in Tropical Forest Fragments. *Conservation Biology* **13**, 1140 - 1150.
- BROWN, E. & KEPHART, S. (1999). Variability in pollen load: implications for reproduction and seedling vigor in a rare plant, *Silene Dougladii* Var. *Oraria*. *International Journal of Plant Sciences* **160**, 1145-1152.
- BUCHMANN, S. L. & NABHAN, G. P. (1996). *The Forgotten Pollinators*. Island Press, Washington D.C.
- BURD, M. (1994). Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* **60**, 83-139.
- BYERS, D. L. (1995). Pollen quantity and quality as explanations for low seed set in small populations exemplified by *Eupatorium* (Asteraceae). *American Journal of Botany* **82**, 1000-1006.
- CANE, J. H. (2001). Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* **5**, 3 [online] URL: <http://www.consecol.org/vol5/iss1/art3>.
- CASCANTE, A., QUESADA, M., LOBO, J. J. & FUCHS, E. A. (2002). Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea sama*. *Conservation Biology* **16**, 137-147.
- CBD. (1992). Convention on Biological Diversity (CBD), Rio de Janeiro, Brasil.
- CBD. (1996). Decision III/11: Conservation and Sustainable Use of Agricultural Biological Diversity (COP3). In *Third Meeting of the Conference of the Parties*, Nairobi, Kenya.
- CHAPIN, F. S. I., ZAVALA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALA, O. E., HOBBI, S. E., MACK, M. C. & DIAZ, S. (2000). Consequences of changing biodiversity. *Nature* **405**, 234 - 242.
- CINCOTTA, R. P., WISNEWSKI, J. & ENGELMAN, R. (2000). Human population in the biodiversity hotspots. *Nature* **404**, 990-992.

- CLAUSNITZER, V. (2004). Diversity and species composition of Odonata as indicators of biotope quality of East African rain forests and their replacement communities. In: *BIOTA East Africa - Biodiversity in conversion - The influence of fragmentation and disturbance on the biodiversity of East African highland rain forests* (ed. J. Köhler), pp. 87-100. BMBF, Bonn.
- COSTIN, B. J., MORGAN, J. W. & YOUNG, A. G. (2001). Reproductive success does not decline in fragmented populations of *Leucochrysum albicans* subsp. *albicans* var. *tricolor* (Asteraceae). *Biological Conservation* **98**, 273-284.
- CUNNINGHAM, S. A. (1996). Pollen supply limits fruit initiation by a rain forest understorey palm. *Journal of Ecology* **84**, 185-194.
- CUNNINGHAM, S. A. (2000a). Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London B-Biological Sciences* **267**, 1149-1152.
- CUNNINGHAM, S. A. (2000b). Effects of habitat fragmentation on the reproductive ecology of four plant species in mallee woodland. *Conservation Biology* **14**, 758-768.
- DEVOTO, M., MEDAN, D. & MONTALDO, N. H. (2005). Pattern of interaction between plants and pollinators along an environmental gradient. *OIKOS* **109**, 461-472.
- DICK, C. W., ETCHOLECU, G. & AUSTERLITZ, F. (2003). Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and Africa honeybees in pristine and fragmented Amazonian rainforest. *Molecular Ecology* **12**, 753-764.
- DIDHAM, R. K., GHAZOUL, J., STORK, N. E. & DAVIS, A. J. (1996). Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* **11**, 255-260.
- DIETZSCH, A. C. (2004). Effects of interspecific pollen transfer on seed set in two East African *Acanthus* species (Acanthaceae). Diploma thesis, Rheinische Friederich-Wilhelms-Universität zu Bonn.
- ERWIN, T. L. (1982). Tropical forests: Their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36**, 74 - 75.
- FAEGRI, K. & VAN DER PIJL, L. (1979). *The Principles of Pollination Ecology*, 3rd edition. Pergamon, Oxford.
- FAO. (1977). *Guidelines for soil profile description*, Rom.
- FARWIG, N. (2005). Impact of forest fragmentation and disturbance on the endangered tropical tree *Prunus africana* (Rosaceae). PhD thesis, Johannes Gutenberg-Universität.
- FISCHER, M. & MATTHIES, D. (1997). Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). *American Journal of Botany* **84**, 1685-1692.
- FISCHER, M. & STÖCKLIN, J. (1997). Local extinctions of plants in remnants of extensively used calcareous grasslands 1950-1985. *Conservation Biology* **11**, 727-737.
- FREUND, W. (2004). Effects of fragmentation and degradation of an afro-tropical rain forest on the diversity structure of leaf beetle communities (Coleoptera, Chrysomelidae). PhD thesis, Rheinische Friedrich-Wilhelms-Universität Bonn.
- GASTON, K. J. (2000). Global patterns in biodiversity. *Nature insight - Biodiversity* **405**, 220 - 227.
- GHAZOUL, J. (2004). Sex in space: pollination among spatially isolated plants. *Biotropica* **36**, 128-130.
- GHAZOUL, J. (2005). Pollen and seed dispersal among dispersed plants. *Biological Reviews* **80**, 413-443.
- GHAZOUL, J. (2006). Floral diversity and facilitation of pollination. *Journal of Ecology* **94**, 295-304.
- GHAZOUL, J. & MCLEISH, M. (2001). Reproductive ecology of tropical forest trees in logged and fragmented habitats in Thailand and Costa Rica. *Plant Ecology* **153**, 335-345.
- GIKUNGU, M. (2006). Bee diversity and some aspects of their ecological interactions with plants in a successional tropical community. PhD thesis, Rheinische Friedrich-Wilhelms-Universität Bonn.
- GOVERDE, M., SCHWEIZER, K., BAUR, B. & ERHARDT, A. (2002). Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biological Conservation* **104**, 293-299.
- GROOM, M. J. (1998). Allee effects limit population viability of an annual plant. *American Naturalist* **151**, 487-496.
- HALL, P., WALKER, S. & BAWA, K. (1996). Effect of Forest Fragmentation on Genetic Diversity and Mating System in a Tropical Tree, *Pithecellobium elegans*. *Conservation Biology* **10**, 757 - 768.
- HARRIS, L. D. (1988). Edge effects and conservation of biotic diversity. *Conservation Biology* **2**, 330-332.
- HARRIS, L. F. & JOHNSON, S. D. (2004). The consequences of habitat fragmentation for plant-pollinator mutualisms. *International Journal of Tropical Insect Science* **24**, 29-43.
- HARRISON, S. & BRUNA, E. (1999). Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography* **22**, 225-232.
- HENDRIX, S. D. & KYHL, J. F. (2000). Population size and reproduction in *Phlox pilosa*. *Conservation Biology* **14**, 304-313.
- HEYWOOD, V. D. (1995). *Global Biodiversity Assessment*. Cambridge University Press, UK.
- HUSTON, M. A. (1994). General Patterns of Species Diversity. In: *Biological Diversity*, pp. 15-62. Cambridge University Press, New York.

- INHAI ANALO, C. (2003). *Adventures of Kakamega Forest*, First edition. BIOTA East Africa E 12, Germany.
- IPI. (1999). International Pollinators Initiative: The Sao Paulo Declaration on Pollinators, pp. 79. Brazilian Ministry of the Environment, Brasilia.
- JACQUEMYN, H., BRYN, R. & HERMY, M. (2002). Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. *Oecologia*, 617-625.
- JANZEN, D. H. (1974). The deflowering of Central America. *Natural History* **83**, 49.
- JENNERSTEN, O. (1988). Pollination in *Dianthus deltoides* (Caryophyllaceae): Effects of Habitat Fragmentation on Visitation and Seed Set. *Conservation Biology* **2**, 359 - 366.
- JULES, E. S. & RATHCKE, B. J. (1999). Mechanisms of reduced *Trillium* recruitment along edges of old-growth forest fragments. *Conservation Biology* **13**, 784-793.
- KAREIVA, P. (1987). Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326**, 388-390.
- KASINA, J. M. (2005). Bee pollinator species in Kakamega Farmlands as affected by distance from the Kakamega Forest edges. (internal & unpublished BIOTA E10 report), Kakamega.
- KEARNS, C. A. & INOUE, D. W. (1993). *Techniques for Pollination Biologists*. University Press of Colorado, Niwot, Colorado.
- KEARNS, C. A., INOUE, D. W. & WASER, N. M. (1998). Endangered mutualism: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**, 83-112.
- KÉRY, M., MATTHIES, D. & SPILLMANN, H.-H. (2000). Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Ecology* **88**, 17-30.
- KEVAN, P. G. (1975). Pollination and environmental conservation. *Environmental Conservation* **2**, 293 - 298.
- KIFCON. (1994). *Kakamega Forest - The Official Guide*. Kenya Indigenous Forest Conservation Programme, Nairobi.
- KNAPP, R. (1973). *Die Vegetation von Afrika*. Fischer, Stuttgart.
- KÖHLER, J. (2004). Synthesis of Phase I. In: *BIOTA East Africa - Biodiversity in conversion - The influence of fragmentation and disturbance on the biodiversity of East African highland rain forests* (ed. J. Köhler), pp. 1-16. BMBF, Bonn.
- KOKWARO, J. O. (1988). Conservation Status of the Kakamega Forest in Kenya: The Easternmost Relic of the Equatorial Rain Forests of Africa. *Monogr. Syst. Bot. Missouri Bot. Gard.* **25**, 471 - 489.
- KOKWARO, J. O. (1994). *Flowering Plant Families of East Africa - An Introduction to Plant Taxonomy*. East African Educational Publishers Ltd., Nairobi.
- KONDOH, M. (2003). Habitat fragmentation resulting in overgrazing by herbivores. *Journal of Theoretical Biology* **225**, 453-460.
- KRAEMER, M. (2002). Auswirkungen von Habitatfragmentierung auf Bestäuber-Pflanzen-Interaktion in ostafrikanischen Regenwäldern. In: *Biodiversity Monitoring Transect Analysis in Africa - Zwischenbericht*, pp. 79-86. BIOTA East Africa Zwischenbericht, Bonn.
- KRAEMER, M. & BERGSDORF, T. (2001). Effects of habitat fragmentation on plant-pollinator interactions in East African rainforests. In: *German Programme on Biodiversity and Global Change (BIOLOG), Annual Report 2001*, pp. 71-77. German Aerospace Research Establishment, Bonn.
- KRAEMER, M., BLEHER, B., BERGSDORF, T. & BÖHNING-GAESE, K. (2001). Threatened mutualisms: pollination, seed dispersal and regeneration in forest remnants. *I. Statusseminar des BIOLOG-Programmes des BMBF*.
- KÜHNE, L., COLLINS, S. C. & KINUTHIA, W. (2004). Check-list of the butterflies of the Kakamega Forest Nature Reserve in western Kenya (Lepidoptera: Hesperioidea, Papilionoidea). *Nachrichten des Entomologischen Vereins Apollo, N.F.* **25**, 161-174.
- LAMONT, B. B., KLINKHAMER, P. G. L. & WITKOWSKI, E. T. F. (1993). Population fragmentation may reduce fertility to zero in *Banksia goodii* - a demonstration of the Allee effect. *Oecologia* **94**, 446 - 450.
- LAURANCE, W. F., VASCONCELOS, H. L. & LOVEJOY, T. E. (2000). Forest loss and fragmentation in the Amazon: implications for wildlife conservation. *Oryx* **34**, 39 - 45.
- LAURANCE, W. F. & YENSEN, E. (1991). Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* **55**, 77-92.
- LEAKEY, R. & MORELL, V. (2002). *Wildlife Wars: My Fight to Save Africa's Natural Treasures*. McMillan Press and St. Martin's Press, London and New York.
- LENNARTSSON, T. (2002). Extinction thresholds and disrupted plant-pollinator interactions in fragmented plant populations. *Ecology* **83**, 3060-3072.
- LIND, E. M. & MORRISON, M. E. S. (1974). *East African Vegetation*. Longman, London.

- LIOW, L. H., SODHI, N. S. & ELMQVIST, T. (2001). Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *Journal of Applied Ecology* **38**, 180-192.
- LLOYD, D. & YATES, J. (1982). Intersexual selection and the segregation of pollen and stigmas in hermaphrodite plants, exemplified by *Wahlenbergia albomarginata* (Campanulaceae). *Evolution* **36**, 903-913.
- LUIJTEN, S. H., DIERICK, A., OOSTERMEIJER, J. G. B., RAIJMANN, L. E. L. & DEN NIJS, C. M. (2000). Population size, genetic variation and reproductive success in a rapidly declining, self-incompatible perennial *Arnica montana* in the Netherlands. *Conservation Biology* **14**.
- LUNG, T. & SCHAAB, G. (2004). Change-detection in Western Kenya - The documentation of fragmentation and disturbance for Kakamega Forest and associated forest areas by means of remotely-sensed imagery. In *ISPRS XXth Congress*, vol. XXXV. ISPRS Archives, Istanbul.
- MANASSE, R. S. & PINNEY, K. (1991). Limits to reproductive success in a partially self-incompatible herb: Fecundity depression at serial life-cycle stages. *Evolution* **45**, 712-720.
- MCDADE, L. A. & MOODY, M. L. (1999). Phylogenetic Relationships Among Acanthaceae: Evidence From Noncoding *TRNL-TRNF* Chloroplast DNA Sequences. *American Journal of Botany* **86**, 70 - 80.
- MICHENER, C. D. (1979). Biogeography of the bees. *Annals of the Missouri Botanical Garden* **66**, 277-347.
- MICHENER, C. D. (2000). *The Bees of the World*. John Hopkins University Press, Baltimore.
- MITCHELL, N. (2004). BIOTA East Report No.1 - The exploitation and disturbance history of Kakamega Forest, Western Kenya. *Bielefelder Ökologische Beiträge Band 20*, 77.
- MONTGOMERY, B. R., KELLY, D., ROBERTSON, A. W. & LADLEY, J. J. (2003). Pollinator behaviour, not increased resources, boosts seed set on forest edges in a New Zealand Loranthaceous mistletoe. *New Zealand Journal of Botany* **41**, 277-286.
- MORGAN, J. W. (1999). Effects of population size on seed production and germinability in an endangered, fragmented grassland plant. *Conservation Biology* **13**, 266-273.
- MURCIA, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10**, 58-62.
- MURIUKI, J. W. & TSINGALIA, M. H. (1990). A new population of de Brazza's monkey in Kenya. *Oryx* **24**, 157 - 162.
- MUSILA, W., DALITZ, H., TODT, H. & USTER, D. (2005). BIOTA East Report No.1 - Soil characteristics of Kakamega Forest, Western Kenya. *Bielefelder Ökologische Beiträge Band 21*.
- MUTANGAH, J. G. (1996). An investigation of vegetation status and process in relation to human disturbance in Kakamega Forest, western Kenya. PhD thesis, University of Wales, UK.
- MYERS, N. (1988). Tropical forests and their species: Going, going ...? In: *Biodiversity* (ed. E. O. Wilson), pp. 28 - 35. National Academy Press, Washington.
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.
- NAEEM, S., CHAIR, F. S., CHAPIN, I. C. R., EHRLICH, P. R., GOLLEY, F. B., HOOPER, D. U., J.H., L., O'NEILL, R. V., MOONEY, H. A., SALA, O. E., SYMSTAD, A. J. & TILMAN, D. (1999). Biodiversity and ecosystem functioning: Maintaining natural life support processes. *Issues in Ecology* **4**, 1-12.
- NASON, J. D. & HAMRICK, J. L. (1997). Reproductive and genetic consequences of forest fragmentation: two case studies of neotropical canopy trees. *The Journal of Heredity* **88**, 264-276.
- NEFF, J. L. & SIMPSON, B. B. (1993). Bees, pollination systems and plant diversity. In: *Hymenoptera and Biodiversity* (ed. J. LaSalle and I. D. Gauld), pp. 143 - 167. CAB international, Wallingford.
- NOVACEK, M. J. & CLELAND, E. E. (2001). The current biodiversity extinction event: scenarios for mitigation and recovery. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5466-5470.
- O'TOOLE, C. & RAW, A. (1999). *Bees of the World*. Blandford, London.
- OLESEN, J. M. & JAIN, S. K. (1994). Fragmented plant populations and their lost interactions. In: *Conservation Genetics* (ed. V. Loeschcke, J. Tomiuk and S. K. Jain). Birkhäuser Verlag, Basel/Switzerland.
- OOSTERMEIJER, J., EUJCK, M. v. & NIJS, J. D. (1994). Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia* **97**, 289-296.
- OOSTERMEIJER, J. G. B., DEN NIJS, J. C. M., RAIJMANN, L. E. L. & MENKEN, S. B. L. (1992). Population biology and management of the marsh gentian (*Gentiana pneumonanthe* L.), a rare species in The Netherlands. *Botanical Journal of the Linnean Society* **108**.
- PACHECO, L. F. & SIMONETTI, J. A. (2000). Genetic structure of a mimosoid tree deprived of its seed disperser, the spider monkey. *Conservation Biology* **14**, 1766 - 1775.

- PERES, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian Forests. *Conservation Biology* **14**, 240 - 253.
- PETERS, M. (2003). Habitatfragmentierung und ihre Auswirkungen auf ostafrikanische Wanderameisen. Diploma thesis, Rheinische Friedrich-Wilhelms-Universität Bonn.
- PIMM, S. L., RUSSEL, G. J., GITTLEMAN, J. L. & BROOKS, T. M. (1995). The future of biodiversity. *Science* **269**, 347-350.
- POTTS, S. G., DAFNI, A. & NE'EMAN, G. (2001). Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. *OIKOS* **92**, 71-80.
- PROCTOR, M., YEO, P. & LACK, A. (1996). *The Natural History of Pollination*, 1 edition. Timber Press, Portland, Oregon.
- QUESADA, M., STONER, E. K., ROSAS-GUERRERO, V., PALACIOS-GUEVARA, C. & LOBO, J. A. (2003). Effects of habitat disruption on the activity of nectarivorous bats (Chiroptera: Phyllostomidae) in a dry tropical forest: implications for the reproductive success of the neotropical tree *Ceiba grandiflora*. *Oecologia* **135**, 400-406.
- RAMSEY, M. & VAUGHTON, G. (2000). Pollen quality limits seed set in *Burchardia umbellata* (Colchicaceae). *American Journal of Botany* **87**, 845-852.
- RATHCKE, B. J. & JULES, E. S. (1993). Habitat fragmentation and plant-pollinator interactions. *Current Science* **65**, 273 - 277.
- RICHARDS, C. M. (2000). Inbreeding depression and genetic rescue in a plant metapopulation. *American Naturalist* **155**, 383-394.
- RICHARDS, C. M., CHURCH, S. & MCCAULEY, D. E. (1999). The influence of population size and isolation on gene flow by pollen in *Silene alba*. *Evolution* **53**, 63-73.
- ROCHA, O. J. & AGUILAR, G. (2001). Reproductive biology of the dry forest tree *Enterolobium cyclocarpum* (Guanacaste) in Costa Rica: a comparison between trees left in pastures and trees in continuous forest. *American Journal of Botany* **88**, 1607-1614.
- RODGER, J., BALKWILL, K. & GEMMILL, B. (2004). African Pollination Studies: where are the gaps? *International Journal of Tropical Insect Science* **24**, 5-28.
- ROLAND, J. (1993). Larger-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**, 25-30.
- ROTHMAN, L. D. & ROLAND, J. (1998). Forest fragmentation and colony performance of forest tent caterpillar. *Ecography* **21**, 383-391.
- ROUBIK, D. W. (1989). *Ecology and Natural History of Tropical Bees*. Cambridge University Press.
- ROUBIK, D. W. (2001). Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology* **5**, 2 [online] URL: <http://www.consecol.org/vol5/iss1/art2>.
- SACHS, J. (2005). *The End of Poverty*. Penguin Group, London.
- SALA, O. E., CHAPIN III, F. S., ARMESTO, J. J., BERLOW, E., BLOOMFIELD, J., DIRZO, R., HUBER-SANWALD, E., HUENNEKE, L. F., JACKSON, R. B., KINZIG, A., LEEMANS, R., LODGE, D. M., MOONEY, H. A., OESTERHELD, M., POFF, N. L., SYKES, M. T., WALKER, B. H., WALKER, M. & WALL, D. H. (2000). Global Biodiversity Scenarios for the year 2100. *Science* **287**, 1770-1774.
- SAUNDERS, D. A., HOBBS, R. J. & MARGULES, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**, 18-32.
- SAYER, J. A., HARCOURT, C. S. & COLLINS, N. M. (1992). *The Conservation Atlas of Tropical Forests: Africa*. United Kingdom by Macmillan Publishers Ltd., Basingstoke, UK.
- SCHEMSKE, D. W. & HORVITZ, C. C. (1988). Plant-animal interactions and fruit production in a neotropical herb: a path analysis. *Ecology* **69**, 1128-1137.
- SCHMITT, J. (1983). Density-dependent pollinator foraging, flowering phenology, and temporal pollen dispersal patterns in *Linanthus bicolor*. *Evolution* **37**, 1247-1257.
- SCHULKE, B. & WASER, N. M. (2001). Long-distance pollinator flights and pollen dispersal between populations of *Delphinium nuttallianum*. *Oecologia* **127**, 239-245.
- SEVERNS, P. (2003). Inbreeding and small population size reduce seed set in a threatened and fragmented plant species, *Lupinus sulphureus* ssp *kincaidii* (Fabaceae). *Biological Conservation* **110**, 221-229.
- SITTE, P., ZIEGLER, H., EHRENDORFER, F. & BRESINSKY, A. (1991). *Strasburger, Lehrbuch der Botanik*. Gustav-Fischer Verlag.
- SMITH-RAMIREZ, C. & ARMESTO, J. J. (2003). Foraging behaviour of bird pollinators on *Embothrium coccineum* (Proteaceae) trees in forest fragments and pastures in southern Chile. *Austral Ecology* **28**, 53-60.
- SNOW, A. (1986). Pollination dynamics in *Epilobium canum* (Onagraceae): consequences for gametophytic selection. *American Journal of Botany* **73**, 139-151.

- SPEARS, E. E. (1987). Island and mainland pollination ecology of *Centrosoma virginianum* and *Opuntia stricta*. *Journal of Ecology* **75**, 351-362.
- STEFFAN-DEWENTER, I., KLEIN, A.-M., GAEBELE, V., ALFERT, T. & TSCHARNTKE, T. (2006). Bee diversity and plant-pollinator interactions in fragmented landscapes. In: *Plant-Pollinator Interactions - From specialization to generalization* (ed. N. M. Waser and J. Ollerton). The University of Chicago Press, London.
- STEFFAN-DEWENTER, I., MÜNZENBERG, U. & BUERGER, C. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83**, 1421-1432.
- STEFFAN-DEWENTER, I. & TSCHARNTKE, T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia* **121**, 432-440.
- TATTERSFIELD, P., SEDDON, M. B. & LANGE, C. N. (2001). Land-snail faunas in indigenous rainforest and commercial forestry plantations in Kakamega Forest, western Kenya. *Biodiversity and Conservation* **10**, 1809-1829.
- TOTLAND, O., ANDERSON, H. L., BJELLAND, T., DAHL, V., EIDE, W., HOUGE, S., PEDERSEN, S. T. R. & VIE, E. U. (1998). Variation in pollen limitation among plants and phenotypic selection on floral traits in an early spring flowering herb. *OIKOS* **82**, 491-501.
- TSINGALIA, M. H. (1988). Animals and the regeneration of an African rainforest tree. PhD thesis, University of California, USA.
- TURNER, I. M. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33**, 200-209.
- UNDERWOOD, A. (1997). *Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance*. University Press, Cambridge.
- VILLARD, M.-A. (2002). Habitat fragmentation: major conservation issue or intellectual attractor? *Ecological Applications* **12**, 319-320.
- WADE, T. G., RIITERS, K. H., WICKHAM, J. D. & JONES, B. K. (2003). Distribution and Causes of Global Forest Fragmentation. *Conservation Ecology* **7**, 7 [online] URL: <http://www.consecol.org/vol7/iss2/art7>.
- WAGNER, P. (2004). Systematik und Zoogeographie der Reptilienfauna des Kakamega Forest in Kenia. Diploma thesis, Rheinische-Friedrich-Wilhelms-Universität.
- WALLACE, A. R. (1878). *Tropical nature and other essays*. Macmillan, London.
- WASER, N. & PRICE, M. V. (1991). Outcrossing distance effects in *Delphinium nelsonii*: pollen loads, pollen tubes, and seed set. *Ecology* **72**, 171-179.
- WASS, P. (1995). *Kenya's indigenous forests - status, management and conservation*. IUCN, Gland, Switzerland.
- WHITE, F. (1983). *The vegetation of Africa*. UNESCO, Paris.
- WHITMORE, T. C. (1997). Tropical forest disturbance, disappearance and species loss. In: *Tropical forest remnants: Ecology, management, and conservation of fragmented communities* (ed. W. L. Laurence and R. O. Bierregaard Jr.), pp. 3-12. University of Chicago Press.
- WILSON, E. O. (1988). The Current State of Biological Diversity. In: *Biodiversity* (ed. E. O. Wilson), pp. 3-18. National Academy Press, Washington.
- WOLF, A., BRODMANN, P. A. & HARRISON, S. (1999). Distribution of the rare serpentine sunflower, *Helianthus exilis* (Asteraceae), the roles of habitat availability, dispersal limitation and species interactions. *OIKOS* **84**.
- WRI. (2005). *Millennium Ecosystem Assessment, Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC.
- WRIGHT, S. J., ZEBALLOS, H., DOMINGUEZ, I., GALLARDO, M. M., MORENO, M. C. & IBANEZ, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a neotropical forest. *Conservation Biology* **14**, 227-239.

Appendix

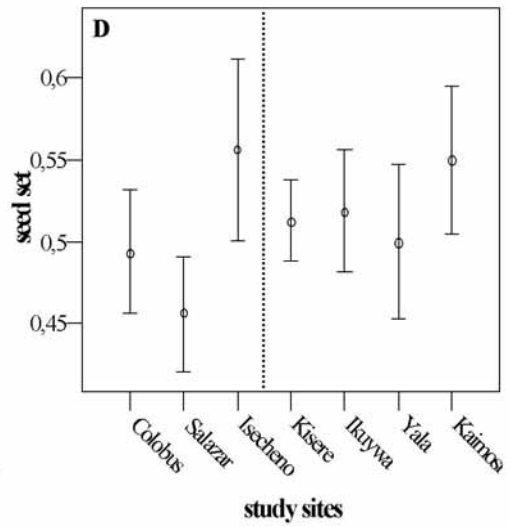
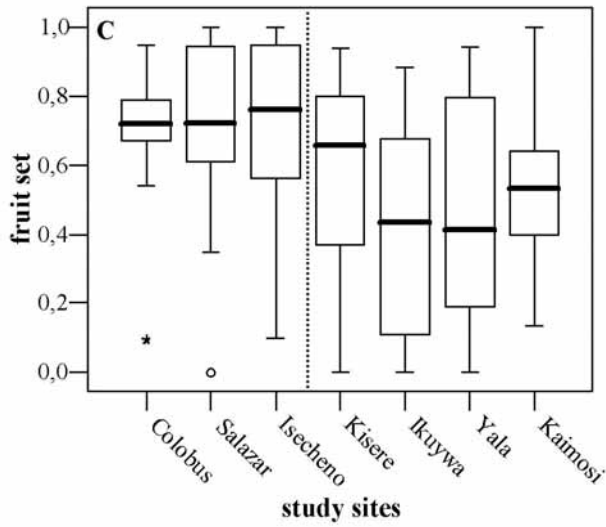
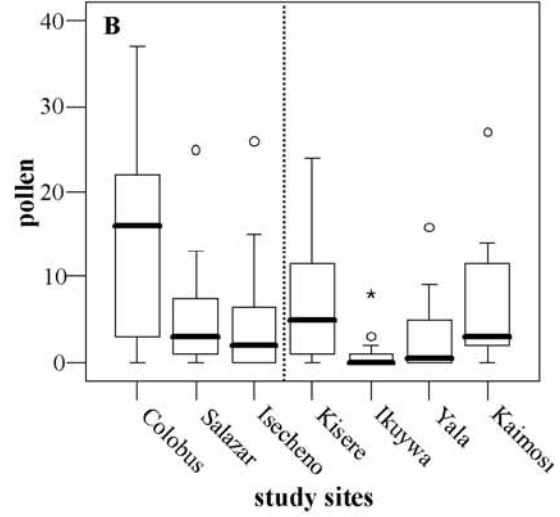
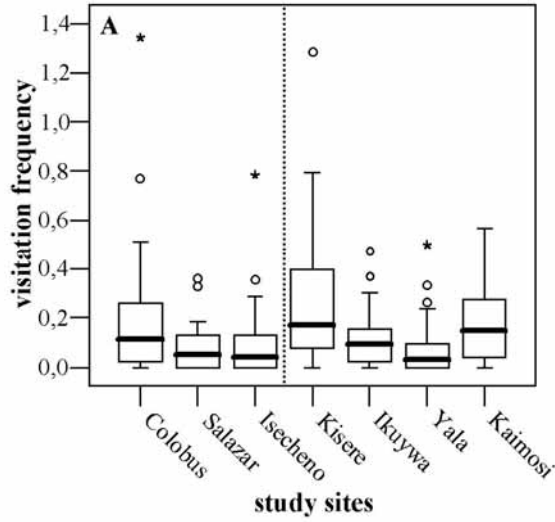
Appendix 1: Levels of pollination in study sites (*Acanthopale pubescens*):

(A) visitation frequencies,

(B) pollen on stigmas,

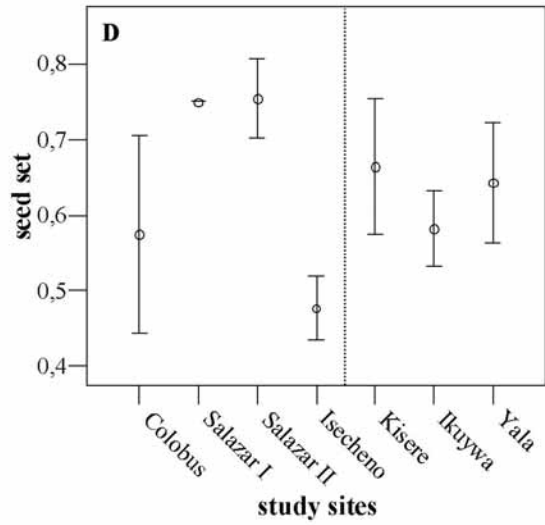
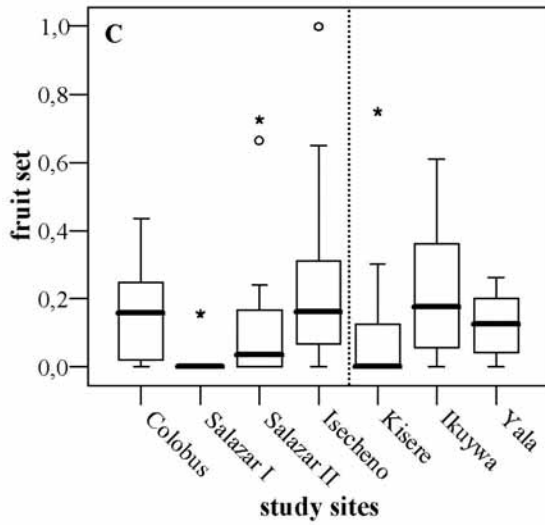
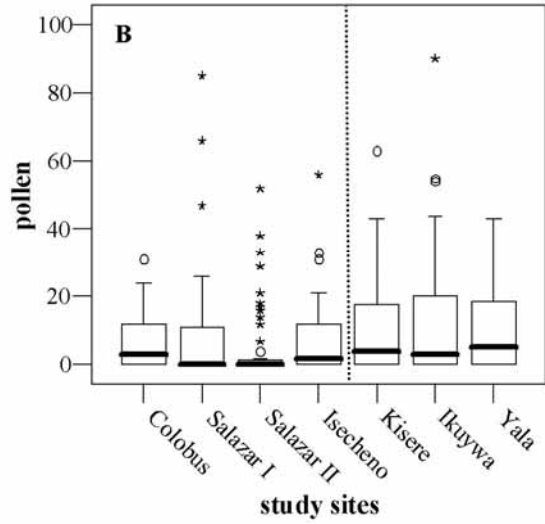
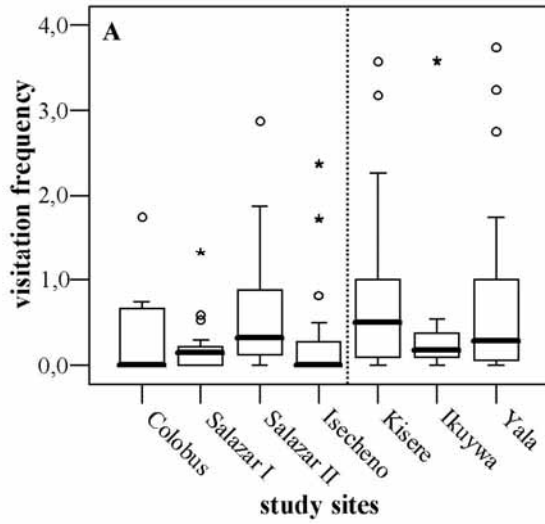
(C) fruit set,

(D) seed set



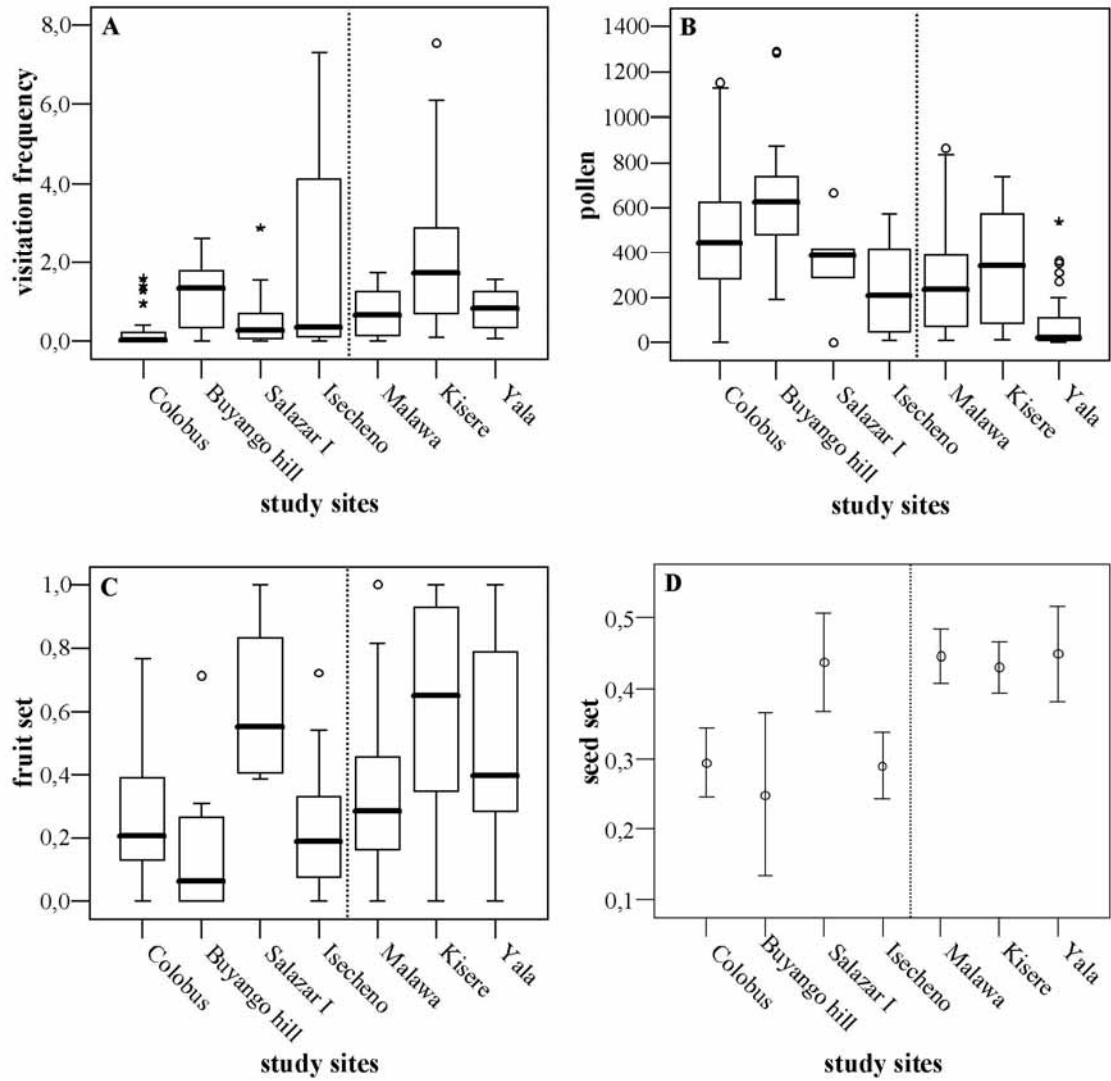
Appendix 3: Levels of pollination in study sites (*Acanthus eminens*) (campaign 2003):

- (A) visitation frequencies,
- (B) pollen on stigmas,
- (C) fruit set,
- (D) seed set



Appendix 4: Levels of pollination in study sites (*Heinsenia diervilleoides*):

- (A) visitation frequencies,
 (B) pollen on stigmas,
 (C) fruit set,
 (D) seed set

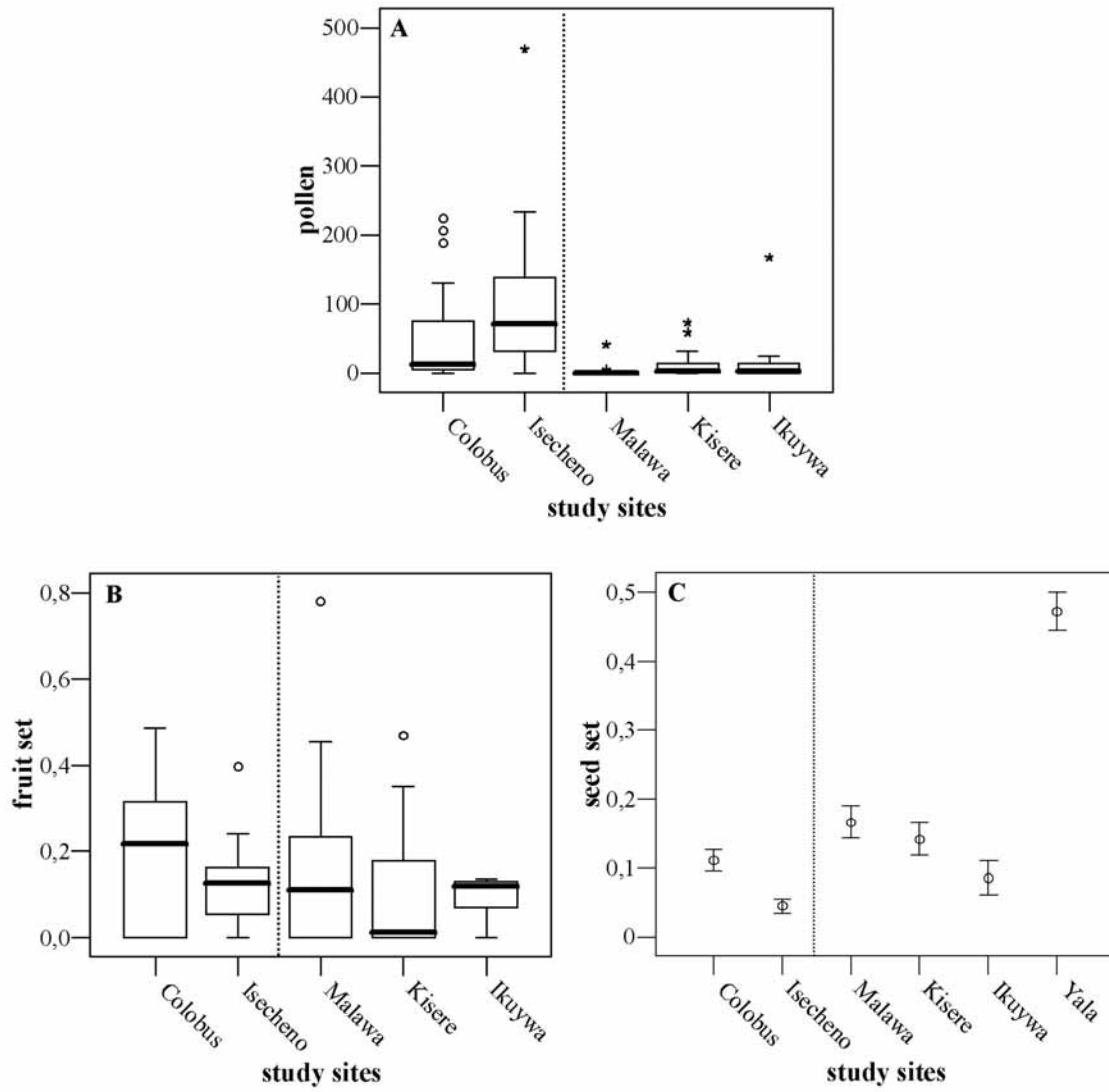


Appendix 5: Levels of pollination in study sites (*Dracaena fragrans*):

(A) pollen on stigmas,

(B) fruit set,

(C) seed set



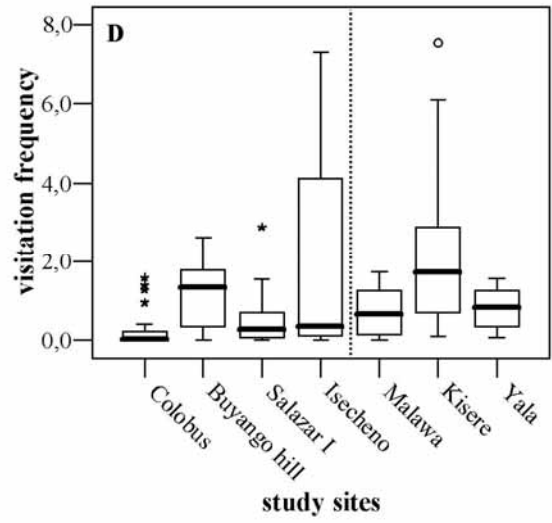
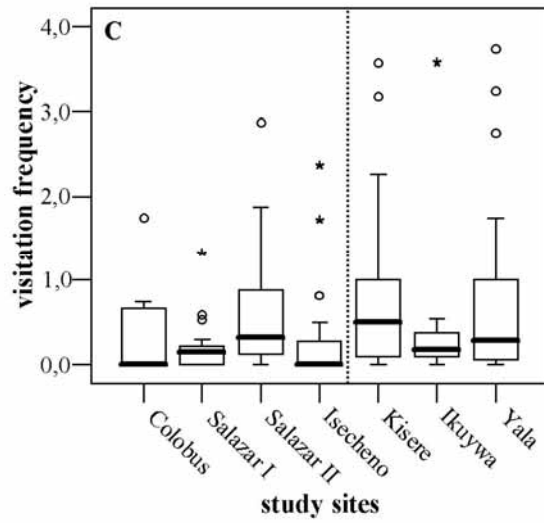
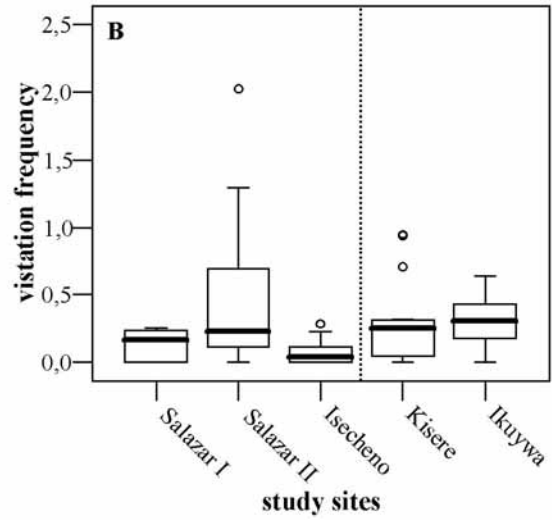
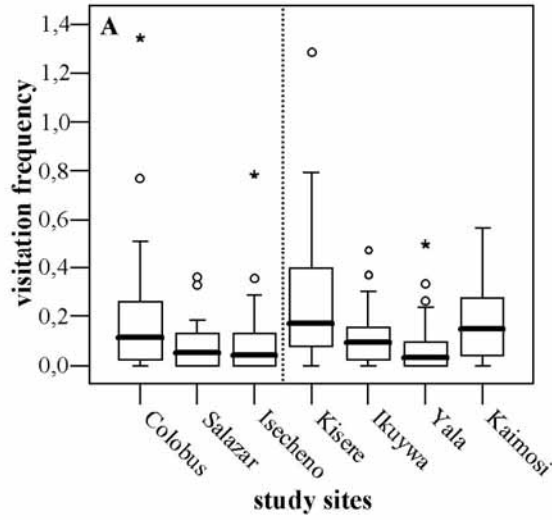
Appendix 6: Visitation frequency in study sites:

(A) *Acanthopale pubescens*,

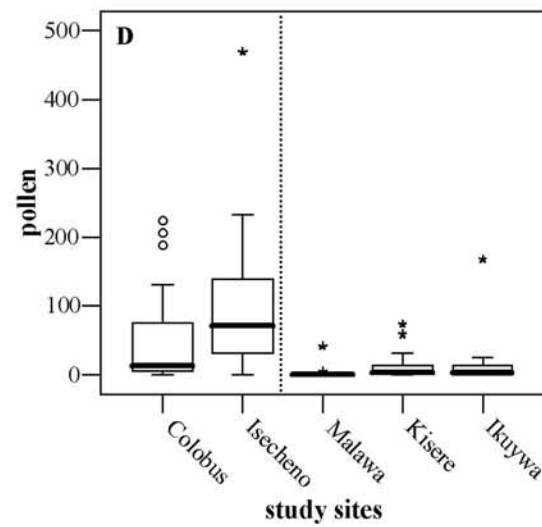
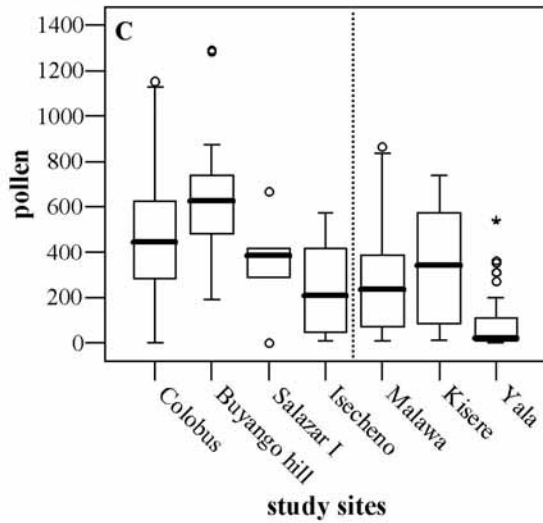
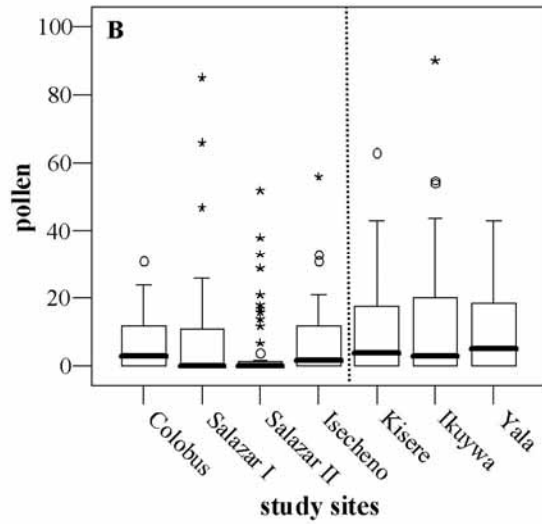
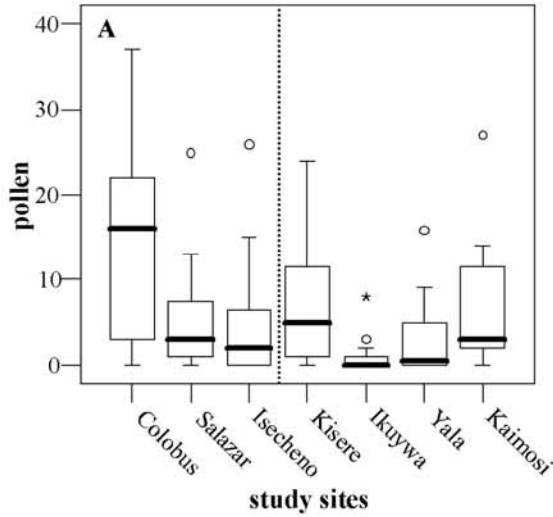
(B) *Acanthus eminens* (campaign 2002),

(C) *Acanthus eminens* (campaign 2003),

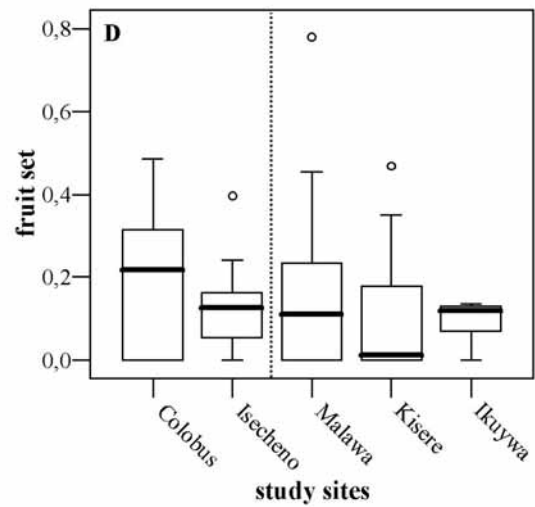
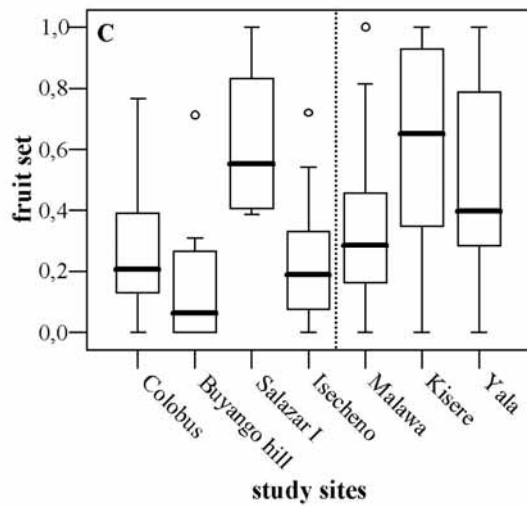
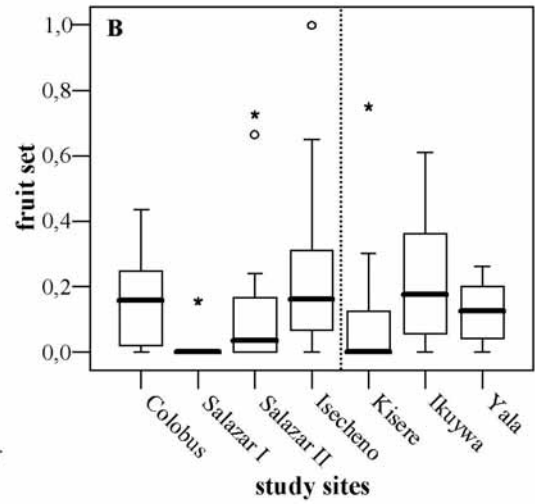
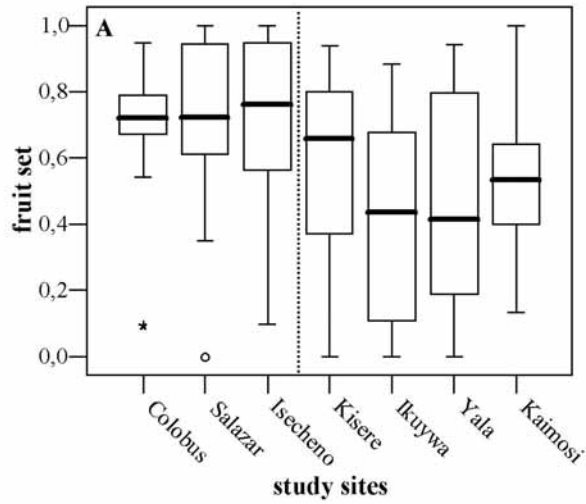
(D) *Heinsenia diervilleoides*



Appendix 7: Pollen on stigmas in study sites:
(A) *Acanthopale pubescens*,
(B) *Acanthus eminens* (campaign 2003),
(C) *Heinsenia diervilleoides*,
(D) *Dracaena fragrans*



Appendix 8: Fruit set in study sites:

(A) *Acanthopale pubescens*,(B) *Acanthus eminens* (campaign 2003),(C) *Heinsenia diervilleoides*,(D) *Dracaena fragrans*

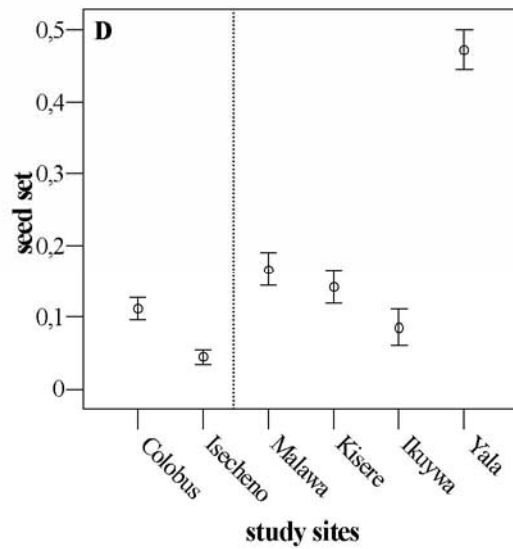
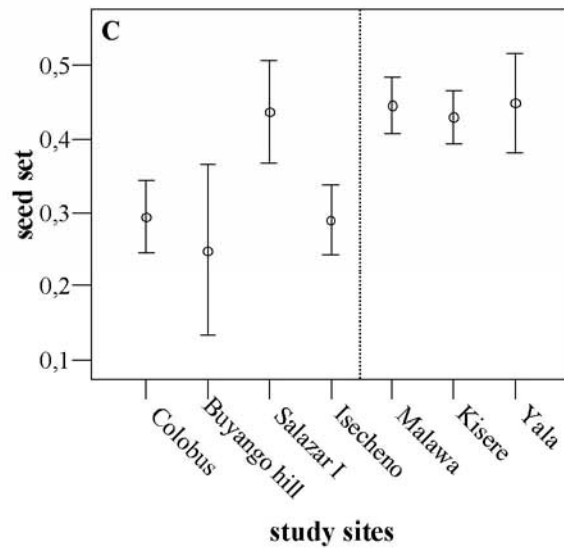
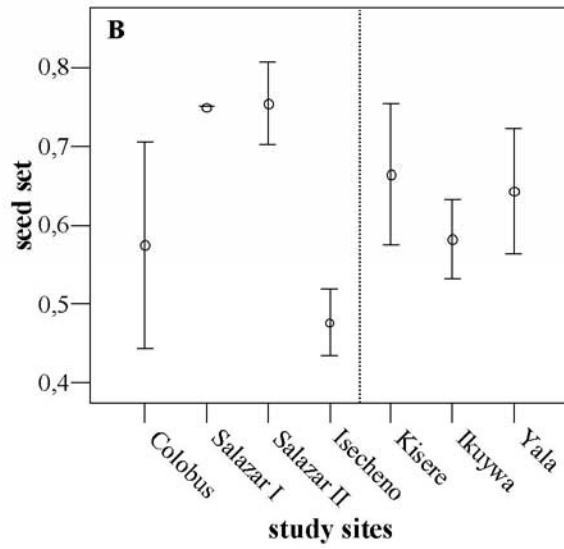
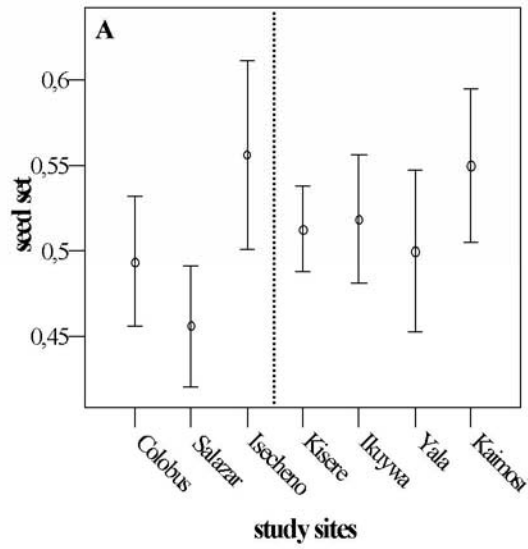
Appendix 9: Seed set in study sites:

(A) *Acanthopale pubescens*,

(B) *Acanthus eminens* (campaign 2003),

(C) *Heinsenias diervilleoides*,

(D) *Dracaena fragrans*



Appendix 10: List of all tested biotic and abiotic factors (see also 5.6 and 5.7)

Biotic factors	Abiotic factors
number of observed flowers	management type
abundance of the plant species	protection status
plant species richness	size of forest fragments
Shannon-Wiener index of species diversity	north-south gradient
fragmentation (main forest or fragment study sites)	paths per ha
succession stages	humidity
% of forest in a 100m buffer	temperature
% of forest in a 500m buffer	cloudiness
% of forest in a 1,000m buffer	pH-value (soil)
% of forest in a 2,000m buffer	C/N ratio (soil)
cut trees per ha	CEC (soil)
	[Ca ⁺⁺] (soil)
	[Mg ⁺⁺] (soil)

Appendix 11: List of all significantly correlated factors with respect to the visitation frequency of *Acanthopale pubescens* (Pearson correlations) (factors which were considered in the backward multiple regression in boldface)

Factor	r	p
buffer 2000m	-.230**	< 0.001
north-south gradient	-.220**	< 0.001
C/N ratio	.245**	< 0.001
humidity	-.290**	< 0.001
number of observed flowers	-.206**	0.001
management type	-.187**	0.001
pH-value	-.177**	0.005
buffer 500m	-.157*	0.012
cut trees per ha	.132*	0.036
succession stages	-.127*	0.043

Appendix 12: List of collinear factors (if $R^2 > 0.7$) with respect to the visitation frequency of *Acanthopale pubescens*

Factors	R^2
management type/ north-south gradient	.794
buffer 500m/ buffer 2000m	.825
buffer 500m/ pH-value	.893
buffer 2000m/ pH-value	.885

Appendix 13: List of all significantly correlated factors with respect to the number of pollen on stigmas of *Acanthopale pubescens* (Pearson correlations) (factors which were considered in the backward multiple regression in boldface)

Factor	r	p
management type	-.287**	0.001
C/N ratio	.245**	0.002
north-south gradient	-.220**	0.004
protection status	-.186*	0.026

Appendix 14: List of collinear factors (if $R^2 > 0.7$) with respect to the number of pollen on stigmas of *Acanthopale pubescens*

Factors	R^2
management type/ north-south gradient	.715

Appendix 15: List of all significantly correlated factors with respect to the fruit set of *Acanthopale pubescens* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
size of forest fragments	-.331*	< 0.001
fragmentation (main forest or fragment study sites)	-.350**	< 0.001
plant species richness	.265**	0.002
protection status	-.253**	0.003
north-south gradient	-.216*	0.010
management type	-.200*	0.018
buffer 100m	-.179*	0.034

Appendix 16: List of collinear factors (if $R^2 > 0.7$) with respect to the fruit set of *Acanthopale pubescens*

Factors	R^2
fragmentation (main forest or fragment study sites)/ size of forest fragments	.986

Appendix 17: List of all significantly correlated factors with respect to the seed set of *Acanthopale pubescens* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
paths per ha	.212**	< 0.001
abundance of the plant species	.191**	0.001
buffer 1000m	-.177**	0.003
cut trees per ha	.171**	0.004
buffer 100m	-.167**	0.005
buffer 2000m	-.168**	0.005
management type	-.163**	0.006
buffer 500m	-.162**	0.007
pH-value	-.158**	0.008

Appendix 18: List of collinear factors (if $R^2 > 0.7$) with respect to the seed set of *Acanthopale pubescens*

Factors	R²
buffer 500m/ buffer 1000m	.884
buffer 500m/ buffer 2000m	.872
buffer 500m/ cut trees per ha	.740
buffer 2000m/ pH-value	.926
buffer 1000m/ buffer 2000m	.768
buffer 1000m/ cut trees per ha	.816
buffer 1000m/ pH-value	.915
buffer 2000m/ pH-value	.901
cut trees per ha/ abundance of the plant species	.805
cut trees per ha/ pH-value	.759
paths per ha/ abundance of the plant species	.746

Appendix 19: List of all significantly correlated factors with respect to the visitation frequency of *Acanthus eminens* (campaign 2002) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
plant species richness	-.321**	0.006
paths per ha	.262*	0.028
cloudiness	.240*	0.044
cut trees per ha	.238*	0.046

Appendix 20: List of all significantly correlated factors with respect to the visitation frequency of *Acanthus eminens* (campaign 2003) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
succession stages	-.302**	0.008
cloudiness	-.178*	0.021
size of forest fragments	-.171*	0.026
fragmentation (main forest or fragment study sites)	.166*	0.032

Appendix 21: List of collinear factors (if $R^2 > 0.7$) with respect to the visitation frequency of *Acanthus eminens* (campaign 2003)

Factors	R^2
fragmentation (main forest or fragment study sites)/ size of forest fragments	.994

Appendix 22: List of all significantly correlated factors with respect to the number of pollen on stigmas of *Acanthus eminens* (campaign 2002) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	-.183**	0.006
size of forest fragments	.176**	0.008
protection status	-.171**	0.010
pH-value	.172**	0.010
abundance of the plant species	-.169*	0.011
buffer 2000m	.165*	0.013
plant species richness	.166*	0.013
north-south gradient	-.138*	0.038
management type	-.133*	0.046

Appendix 23: List of collinear factors (if $R^2 > 0.7$) with respect to the number of pollen on stigmas of *Acanthus eminens* (campaign 2002)

Factors	R^2
management type/ north-south gradient	.790
fragmentation (main forest or fragment study sites)/ size of forest fragments	.993
fragmentation (main forest or fragment study sites)/ buffer 2000m	.960
fragmentation (main forest or fragment study sites)/ abundance of the plant species	.725
fragmentation (main forest or fragment study sites)/ pH-value	.784
size of forest fragments/ buffer 2000m	.953
size of forest fragments/ pH-value	.790
buffer 2000m/ pH-value	.892

Appendix 24: List of all significantly correlated factors with respect to the number of pollen on stigmas of *Acanthus eminens* (campaign 2003) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	.122*	0.025
buffer 1000m	-.120*	0.028
size of forest fragments	-.119*	0.030

Appendix 25: List of collinear factors (if $R^2 > 0.7$) with respect to the number of pollen on stigmas of *Acanthus eminens* (campaign 2003)

Factors	R^2
fragmentation (main forest or fragment study sites)/ size of forest fragments	.994

Appendix 26: List of all significantly correlated factors with respect to the fruit set of *Acanthus eminens* (campaign 2002) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	.345**	< 0.001
size of forest fragments	-.384**	< 0.001
buffer 1000m	-.380**	< 0.001
buffer 2000m	-.356**	< 0.001
succession stages	-.592**	< 0.001
cut trees per ha	.445**	< 0.001
north-south gradient	-.407**	< 0.001
pH-value	-.355**	< 0.001
humidity	-.469**	< 0.001
CEC	-.505**	< 0.001
[Ca ⁺⁺]	-.505**	< 0.001
C/N ratio	.275**	0.006
buffer 500m	-.269**	0.007
Shannon-Wiener index of species diversity	.267**	0.007
management type	-.214*	0.032

Appendix 27: List of collinear factors (if $R^2 > 0.7$) with respect to the fruit set of *Acanthus eminens* (campaign 2002)

Factors	R²
management type/ north-south gradient	.736
fragmentation (main forest or fragment study sites)/ size of forest fragments	.993
fragmentation (main forest or fragment study sites)/ buffer 500m	.797
fragmentation (main forest or fragment study sites)/ buffer 1000m	.860
fragmentation (main forest or fragment study sites)/ buffer 2000m	.928
fragmentation (main forest or fragment study sites)/ [Ca ⁺⁺]	.779
size of forest fragments/ buffer 500m	.777
size of forest fragments/ buffer 1000m	.871
size of forest fragments/ buffer 2000m	.926
size of forest fragments/ [Ca ⁺⁺]	.836
buffer 500m/ buffer 1000m	.935
buffer 500m/ buffer 2000m	.936
buffer 500m/ buffer 2000m	.947
buffer 1000m/ pH-value	.786
buffer 1000m/ buffer 2000m	.947
buffer 2000m/ pH-value	.848
succession stages/ CEC	.800
succession stages/ [Ca ⁺⁺]	.796
humidity/ CEC	.754
humidity/ [Ca ⁺⁺]	.833
CEC/ [Ca ⁺⁺]	.874

Appendix 28: List of all significantly correlated factors with respect to the fruit set of *Acanthus eminens* (campaign 2003) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
management type	.313**	< 0.001
paths per ha	.299**	0.001
[Mg ⁺⁺]	.292**	0.001
C/N ratio	-.256**	0.004
buffer 100m	-.227*	0.010
north-south gradient	.192*	0.030
protection status	.186*	0.036
CEC	.176*	0.048
pH-value	-.175*	0.049

Appendix 29: List of collinear factors (if $R^2 > 0.7$) with respect to the fruit set of *Acanthus eminens* (campaign 2003)

Factors	R ²
management type/ north-south gradient	.718
management type/ C/N ratio	.740
paths per ha/ [Mg ⁺⁺]	.971

Appendix 30: List of all significantly correlated factors with respect to the seed set of *Acanthus eminens* (campaign 2003) (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
management type	-.241**	< 0.001
buffer 100m	.210**	< 0.001
plant species richness	-.231**	< 0.001
Shannon-Wiener index of species diversity	-.168**	< 0.001
cut trees per ha	-.203**	< 0.001
paths per ha	-.301**	< 0.001
C/N ratio	.251**	< 0.001
CEC	-.192**	< 0.001
[Mg ⁺⁺]	-.291**	< 0.001
pH-value	.163**	0.001
[Ca ⁺⁺]	-.135**	0.005
humidity	-.130**	0.007
succession stages	-.110*	0.023
abundance of the plant species	.104*	0.031

Appendix 31: List of collinear factors (if $R^2 > 0.7$) with respect to the seed set of *Acanthus eminens* (campaign 2003)

Factors	R ²
buffer 100m/ plant species richness	.720
buffer 100m/ Shannon-Wiener index of species diversity	.764
buffer 100m/ abundance of the plant species	.851
abundance of the plant species/ Shannon-Wiener index of species diversity	.816
abundance of the plant species/ cut trees per ha	.725
Shannon-Wiener index of species diversity/ abundance of the plant species	.757
paths per ha/ [Mg ⁺⁺]	.973
CEC/ [Ca ⁺⁺]	.915
C/N ratio/ humidity	.718

Appendix 32: List of all significantly correlated factors with respect to the visitation frequency of *Heinsenias diervilleoides* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
Shannon-Wiener index of species diversity	.362**	< 0.001
cut trees per ha	.375**	< 0.001
succession stages	-.269**	0.001
paths per ha	.269**	0.001
cloudiness	.232**	0.004
abundance of the plant species	.222**	0.006
plant species richness	.192*	0.018
humidity	-.165*	0.042

Appendix 33: List of collinear factors (if $R^2 > 0.7$) with respect to the visitation frequency of *Heinsenias diervilleoides*

Factors	R^2
abundance of the plant species/ cloudiness	.869
cloudiness/ humidity	.754

Appendix 34: List of all significantly correlated factors with respect to the number of pollen on stigmas of *Heinsenias diervilleoides* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
management type	-.497**	< 0.001
fragmentation (main forest or fragment study sites)	-.348**	< 0.001
size of forest fragments	.331**	< 0.001
abundance of the plant species	.323**	< 0.001
pH-value	-.419**	< 0.001
C/N ratio	.442**	< 0.001
humidity	-.456**	< 0.001
north-south gradient	-.209**	0.002
paths per ha	-.202**	0.002
buffer 1000m	.181**	0.007
buffer 100m	.178**	0.008
protection status	-.142*	0.034

Appendix 35: List of collinear factors (if $R^2 > 0.7$) with respect to the number of pollen on stigmas of *Heinsenia diervilleoides*

Factors	R^2
management type/ C/N ratio	.813
protection status/ buffer 1000m	.929
fragmentation (main forest or fragment study sites)/ size of forest fragments	.993
buffer 100m/ paths per ha	.864
C/N ratio/ humidity	.704
humidity/ abundance of the plant species	.858

Appendix 36: List of all significantly correlated factors with respect to the fruit set of *Heinsenia diervilleoides* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	.432**	< 0.001
size of forest fragments	-.431**	< 0.001
buffer 100m	.412**	< 0.001
succession stages	-.336**	< 0.001
abundance of the plant species	.325**	< 0.001
humidity	-.285**	< 0.001
north-south gradient	-.213*	0.016
C/N ratio	.207*	0.019
management type	-.181*	0.040

Appendix 37: List of collinear factors (if $R^2 > 0.7$) with respect to the fruit set of *Heinsenia diervilleoides*

Factors	R^2
management type/ C/N ratio	.926
management type/ humidity	.728
fragmentation (main forest or fragment study sites)/ size of forest fragments	.995
humidity/ C/N ratio	.801
humidity/ abundance of the plant species	.934

Appendix 38: List of all significantly correlated factors with respect to the seed set of *Heinsenias diervilleoides* (Pearson correlations)
(factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	.159**	< 0.001
size of forest fragments	-.159**	< 0.001
buffer 100m	.095**	< 0.001
buffer 1000m	-.093**	< 0.001
plant species richness	-.095**	< 0.001
Shannon-Wiener index of species diversity	-.089**	< 0.001
north-south gradient	-.090**	< 0.001
[Mg⁺⁺]	-.080**	0.002
protection status	.078**	0.003
abundance of the plant species	.075**	0.004
paths per ha	-.070**	0.008
humidity	-.055*	0.034
buffer 2000m	-.052*	0.049

Appendix 39: List of collinear factors (if $R^2 > 0.7$) with respect to the seed set of *Heinsenias diervilleoides*

Factors	R ²
protection status/ buffer 1000m	.738
fragmentation (main forest or fragment study sites)/ size of forest fragments	.996
buffer 1000m/ buffer 2000m	.841
paths per ha/ [Mg ⁺⁺]	.985
humidity/ abundance of the plant species	.921

Appendix 40: List of all significantly correlated factors with respect to the number of pollen on stigmas of *Dracaena fragrans* (Pearson correlations) (factors which were considered in the backward multiple regression in boldface)

Factor	r	p
fragmentation (main forest or fragment study sites)	-.426**	< 0.001
size of forest fragments	.429**	< 0.001
buffer 100m	-.414**	< 0.001
buffer 1000m	.325**	< 0.001
buffer 2000m	.439**	< 0.001
plant species richness	.452**	< 0.001
Shannon-Wiener index of species diversity	.369**	< 0.001
north-south gradient	.391**	< 0.001
paths per ha	.361**	< 0.001
pH-value	.338**	< 0.001
humidity	.416**	< 0.001
protection status	-.239**	0.004
management type	.222**	0.007
buffer 500m	.221**	0.008
cut trees per ha	.191*	0.021

Appendix 41: List of collinear factors (if $R^2 > 0.7$) with respect to the number of pollen on stigmas of *Dracaena fragrans*

Factors	R^2
management type/ paths per ha	.702
management type/ pH-value	.863
fragmentation (main forest or fragment study sites)/ size of forest fragments	.996
buffer 100m/ pH-value	.810
buffer 100m/ humidity	.945
buffer 500m/ buffer 2000m	.703
buffer 2000m/ plant species richness	.867
plant species richness/ Shannon-Wiener index of species diversity	.906
paths per ha/ pH-value	.876
paths per ha/ humidity	.875
pH-value/ humidity	.814

Appendix 42: List of all significantly correlated factors with respect to the seed set of *Dracaena fragrans* (Pearson correlations) (factors which were considered in the backward multiple regression in boldface)

Factor	r	p
management type	.147**	< 0.001
fragmentation (main forest or fragment study sites)	.348**	< 0.001
size of forest fragments	-.324**	< 0.001
buffer 100m	.250**	< 0.001
buffer 500m	.185**	< 0.001
buffer 1000m	.091**	< 0.001
buffer 2000m	.246**	< 0.001
plant species richness	-.365**	< 0.001
Shannon-Wiener index of species diversity	-.122**	< 0.001
succession stages	-.164**	< 0.001
cut trees per ha	-.382**	< 0.001
north-south gradient	.308**	< 0.001
paths per ha	-.400**	< 0.001
pH-value	.191**	< 0.001
C/N ratio	-.072**	< 0.001
humidity	.231**	< 0.001
CEC	-.146**	< 0.001
[Ca ⁺⁺]	-.133**	< 0.001
[Mg⁺⁺]	-.393**	< 0.001
protection status	-.056**	0.006

Appendix 43: List of collinear factors (if $R^2 > 0.7$) with respect to the the seed set of *Dracaena fragrans*

Factors	R²
management type/ pH-value	.846
management type/ CEC	.711
management type/ [Ca ⁺⁺]	.723
fragmentation (main forest or fragment study sites)/ size of forest fragments	.991
buffer 500m/ buffer 1000m	.719
buffer 500m/ buffer 2000m	.814
buffer 500m/ succession stages	.711
buffer 2000m/ north-south gradient	.791
plant species richness/ Shannon-Wiener index of species diversity	.765
cut trees per ha/ paths per ha	.707
paths per ha/ [Mg ⁺⁺]	.992
pH-value/ humidity	.860
CEC/ [Ca ⁺⁺]	.974

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