Effects of fragmentation and degradation of an afrotropical rain forest on the diversity structure of leaf beetle communities (Coleoptera, Chrysomelidae)

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Für meinen geliebten Vater, Hans Christian Freund
(*1933 − †1990)

Chochote chaweza kutukea – Anything can happen anytime

Kenianisches Sprichwort

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1. Introduction

Tropical rain forests, which cover only six to seven per cent of the earth's landmass, deserve our particular attention and protection, since they probably contain 50 % of the global biodiversity (Myers 1979, Wilson 1988, Linsenmair 1990, Bierregaard et al. 2001). The loss of these 'biodiversity hotspots' (Myers 1988, Barthlott et al. 1999, Myers et al. 2000) would mean extinction of a tremendous number of species, although they can receive protection with a comparative low expenditure of money and staff. Despite strong efforts of scientists and politicians, many of these regions are highly endangered. With losses of more than five million hectares per year, accounting for 56 % of the global reduction in forest cover (FAO 2003), African forests are among the most threatened ecosystems worldwide (Achard et al. 2002, Groombridge & Jenkins 2002). East African forests are particularly diverse and endangered but are still little-known ecosystems. Distributed over a highly variable landscape dominated by savannas and thorn bushes, these forests are outstandingly species rich as well as centres of endemism (Fjeldsa & Lovett 1997). They play an important role as cultural heritages and are a traditionally and intensively used resource for the local populations (UNEP 2002). With an increase of the human population in East Africa throughout the last decades, the pressure on biodiversity largely increased and the use of the forest ecosystems is far from being sustainable. Generally, there is no doubt on a local and governmental level that at least core areas of tropical forests need to be maintained and conserved for future generations.

1.1. Evolution of African forests

It has been suggested that African forests once contained a more diverse fauna and flora, but suffered from extinction processes at times of severe climate changes, especially during dry phases of the Quaternary (Stein & Sarnthein 1984). The forest cover in tropical Africa was strongly affected by climate changes during the Holocene and was at its minimum during the cooler and more arid periods of the ice ages (Hamilton 1992). At this time they were confined to a number of relatively small refugia, isolated from each other, at orographically favoured places, e.g. the mountains of Kenya (Hamilton 1992). Rain forest occurred only at specific altitudes in these mountains, because both open country and high mountain regions became too dry and cold, respectively. During warmer and wetter conditions lowland forest cover could spread from those refugia. The maximum postglacial spread of forests in tropical Africa was attained some thousand years after 10000 BP (before present). Comparisons of pollen from deep-sea cores (e.g. van Campo et al. 1982) and meteorological models of

climatic change (Rossignol-Strick 1983) revealed that most, though not all, ice ages resulted in dry periods in tropical Africa, characterised by forest reduction (for climatic change see also Thompson et al. 2002). The severity of the arid periods increased during the Quaternary (Stein & Sarnthein 1984) and a period of generally drier climatic conditions started about 4000 years ago (Hamilton 1992, Thompson et al. 2002). During interglacial periods wetter conditions returned, correlated with forest expansion. The alternate advances and retreats throughout the last millennia led to a natural fragmentation of the forests. This state of natural forest reduction was enhanced by forest clearance through activities of iron-working agriculturalists at about 2200 BP and was still continued by the local people in the last centuries. Today, African forests are the most shrunken forests of the world with only about one-third of their historical extension remaining and representing less than one-fifth of the total remaining resources (Asia more than 1/5, Latin America about 3/5) (Collins 1992). For the conservation and sustainable use of African biodiversity throughout the 21st century it will be of major importance to understand diversity and ecosystem processes within these forests.

At the beginning of the 20th century there were 240,000 ha of lowland rain forest in Kenya, where the present study was conducted. Recently there are only 23,000 ha left due to severe deforestation and fragmentation. In most of these parts a very high anthropogenic impact occurs, resulting in a significant loss of forested areas and decreasing diversity. One of these areas is the Kakamega Forest in western Kenya (Fig. 2). It has provided numerous and invaluable resources to the surrounding people for hundred of years. By the beginning of the last century people had settled around the forest and were farming as much in the forest as around it (Mitchell 2004). Although the forest is protected as a government reserve, the Luhya people, who live in areas surrounding the forest, still rely heavily on the forest for basic needs such as fuelwood, charcoal, timber and other building materials. Owing to these activities the remaining forest is degraded by selective logging, charcoaling, cattle grazing, hunting and debarking of medical plants (Emmerton 1991, Oyugi 1996, Bennun & Njoroge 1999). These processes lead to a transformation of the natural habitat into a fragmented forest mosaic, reduction of the forest fragments sizes and increasing isolation of these fragments (Villard 2002). In addition, the depleting of forested land is supported by the encroachment of shambas (small farms) and tea plantations as well as illegal harvesting of wood. The combined effects of deforestation agents have led to a process commonly referred to as ecosystem decay (Lovejoy et al. 1983) which has been responsible for a drastic reduction in the size of the indigenous forest patches, changes in their structure and diversity and alteration of regeneration mechanisms of forest species. Also plant composition in the small fragments differs from the primary forest (Tabarelli et al. 1999)

and tree mortality is increased in small fragments as well as on forest edges (Williams-Linera 1990b, Laurance et al. 1998, Mesquita et al. 1999). Fragmentation and associated human impact increase the susceptibility of the forest canopy to pest outbreaks, causing defoliation and in some cases the death of the trees (Bellinger et al. 1989, Landsberg 1990, Roland 1993). The loss of insect predators or parasitoids in fragmented habitats has also been shown to release phytophagous insects from natural control, leading to population outbreaks and habitat damage (Kareiva 1987, Lasalle & Gauld 1991, Kruess & Tscharntke 1994).

By increasing expansion of settled areas, all rain forest organisms are increasingly dependent on habitat fragments, which are much smaller than former forests. The original number of species in small fragments is probably reduced, a phenomenon known as "relaxation" (Diamond 1972). Habitat fragmentation, reduction of fragment size, increasing isolation of the fragments and the distance of fragments to the main forest affect diversity, abundance and the risk of extinction of populations (Turner 1996, Debinski & Holt 2000, Laurance et al. 2002). Reduction of habitat size is of importance, because the population density of a species is reduced in smaller habitats. Smaller, isolated populations are more endangered by stochastic fluctuations and genetic drift (Jaenike 1973, Shaffer 1981, Gilpin & Soulé 1986, Pimm et al. 1988). A change of migration processes due to reduced habitat areas (Jaenike 1973, Fahrig & Merriam 1994) leads to reduced gene flow and abundance in many species, also increasing the probability and risk of extinction. For that reason, one of the most important questions of nature conservation is, to what extent are these fragments able to maintain the biodiversity of the continuously forested areas (Laurance & Bierregaard 1997) and how long will the faunal relaxation of fragments take (Brooks et al. 1999).

1.2. How many species are there?

At this point the question arises, how many species do the rain forests maintain. A reply to this question is not very easy, since arthropod communities in tropical rain forests still remain deficiently investigated and described because of their enormous numbers and the lack of taxonomic expertise. While most of the species in Europe are well known and descriptions of new species have become rare, the discovery and description of new species from tropical rain forests is a race against deforestation and destruction of these biomes. More than 20 years ago the question about species richness in the tropics became highly debated due to the influential paper by Erwin (1982). Starting from 1.5 to 2 million recent animal species, Erwin estimated the diversity of tropical forest arthropods to be 30 million species. Based on this paradigmatic change, further

authors estimated the global number of species are ranging from five up to 80 million species (e.g. Erwin 1982, Stork 1988, Wilson 1988). It became clear that the upper limit of such estimates was too optimistic. One of the reasons for the overestimated species numbers was due to the arbitrarily chosen parameters of the calculation like the proportion of specialized phytophagous insects (Erwin 1982) and estimates of arthropod species are clearly reduced by lower host specificity (e.g. May 1986, 1990, Thomas 1990, Gaston 1991a, Hodkinson & Casson 1991, Basset 1992b, Hodkinson 1992, Hammond 1994, Simon 1996, Mawdsley & Stork 1997, Novotny et al. 2002b, Ødegard 2003). The question if more specialists than generalists exist is still subject of many discussions (e.g. Novotny et al. 2002b).

Nowadays most estimations on global species diversity range between five and ten million (e.g. May 1986, 1990, Thomas 1990, Gaston 1991b, a, Hodkinson & Casson 1991, Hodkinson 1992, Hammond 1994, Simon 1996). Most of these species live in wet tropical forests (Gaston 2000) and samples from all major tropical regions reveal an enormous species richness and diversity of canopy arthropod communities (e.g. for South and Central America (Erwin & Scott 1980, Erwin 1983, Adis et al. 1984, Davies et al. 1997), for South East Asia (Stork 1987b, a, Morse et al. 1988, Hammond 1990, Stork & Brendell 1990, Floren & Linsenmair 1994, Hammond et al. 1997), for Australia and New Guinea (Basset & Kitching 1991, Allison et al. 1993, Kitching & Arthur 1993) and for Africa (Wagner 2001). The high diversity of vegetation in the tropics and its rich structures of twigs and leaves offer a huge variety of habitats and resources for arthropods. Hence, it follows that an increasing number of ecological licenses generally leads to a larger density of species (Lawton 1983, Williamson & Lawton 1991). Another even simpler cause might be due to climatic conditions. The temperature in the tropics is quite constant throughout the year, frost only occurs in altitudes beyond 3000 m above sea level and thus food is always available and reproduction may occur several times per year. Long periods of "non-productivity" like the hibernation in the temperate zones are not necessary. Nevertheless, rainy seasons and dry seasons are alternating and seasonality has an influence on the natural history in wet forest ecosystems (Wolda 1988, 1992a, Novotny & Basset 1998, Lucky et al. 2002, Wagner 2003).

So the question about the true extent of biodiversity certainly remains unanswered, but no matter how many species actually exist, efforts for their protection should be taken in any case. Scientists and politicians are trying to find strategies for the conservation and sustainable use of biological diversity since 1992, when Germany agreed and signed the International Convention on Biological Diversity (CBD) at the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro. The recommendations emanating from UNCED identified inventory, survey and monitoring

of basic biological resources to be necessary to quantify biodiversity in all nations (Lovejoy 1994). One of the initiatives to develop such strategies is the BIOTA East Africa Project (Biodiversity Monitoring Transect Analysis in Africa) funded within the BIOLOG program (Biodiversity and Global Change) by the German Federal Ministry of Education and Research (BMBF). It is an interdisciplinary project of German and Kenyan scientists and research focuses on two forests in Kenya, namely the Kakamega Forest and forests around Mount Kenya. This study was conducted within the framework of the BIOTA East Africa Project in tight cooperation with the National Museums of Kenya (NMK, Nairobi), World Agroforestry Centre (WAC, Nairobi) and the Kakamega Environmental Education Programme (KEEP, Isecheno).

1.3. Stochasticity versus deterministic equilibrium models

While tropical arthropod communities in tree crowns appear to be enormously species rich, the mechanisms that maintain and regulate these coexistences are still poorly described (Lucky et al. 2002). Two scenarios are known which might regulate the structures of arthropod diversity, namely deterministic equilibrium models on the one hand and stochastic non-equilibrium models on the other hand. In non-equilibrium models, communities are mainly influenced by chance effects (Caswell 1976, Huston 1979, Wiens 1984, Cornell & Lawton 1992, Huston 1994). A fauna characterised by a high number and random distribution of species, together with very low population levels, is typical of non-interactive communities with a high beta-diversity (Schoener 1986, Cornell & Lawton 1992). The biotope is not saturated with species, i.e. there are numerous vacant licences which can be used by randomly immigrating species, or these may be repeatedly vacated as a result of the extinction of small local populations (Kitching et al. 1997). The densities of species might be higher in such a biotope, since population abundances are usually very low (Elton 1973, Lawton 1991, Basset et al. 1992, Basset 2001b). The local faunal community of a habitat does not reach a climax formation and can differ very much from the fauna of an adjacent habitat (Caswell 1978, Connor & Simberloff 1979).

The deterministic equilibrium is based on Darwin's assumption that intra- and interspecific competition is necessary for evolutionary processes (Schoener 1982, Den Boer 1985). Interspecific competition leads to resource partitioning, increasing specialisation and decreasing niche breadths of species and therefore, to an increased number of species and population density in an undisturbed environment. The population density is limited by the size of the habitat and successional stages are leading to climax formations and ends up with structurally predictable climax

equilibrium. Despite migration processes, respectively of speciation and extinction, the numbers of species remain at a constant level (MacArthur & Wilson 1967). Interspecific competition is certainly suitable to explain speciation and diversification of organisms, but if it is really of importance for evolution, especially in the tropics, it is hard to prove (Braakhekke 1985, Jacobs 1985) and just for arthropods quite unlikely.

Generally, it is thought that primary forests are relatively static and deterministic systems, while in secondary forests successions lead to higher dynamics and heterogeneity (Brown & Lugo 1990). This probably leads also to a larger variety of factors in secondary habitats, which influence the structure of biocoenoses. Stochastic processes are certainly of importance in such biocoenoses, where a high proportion of rare species can be found and the local fauna remains mostly incompletely sampled. Moreover, populations of rare species are obviously fluctuating in a chaotic way (May 1975, Vandermeer 1982) and deterministic statements or predictions on the distribution of these species in time and space are not possible.

1.4. Objectives

In some works several groups of arthropods, especially of insects, were studied and used as indicator species with the attempt to measure and monitor organismic biodiversity (e.g. Pyle et al. 1981, Rosenberg et al. 1986, Morris & Rispin 1988, Samways 1988, Viejo et al. 1989, Webb 1989, Den Boer 1990, Samways 1990, Ozanne et al. 1997). Kremen et al. (1993) point out the usefulness of insects in detecting environmental impacts, such as fragmentation, disturbance, habitat modification, ecological disturbance, climate change and chemical pollution. Insects are important members of tropical forest ecosystems, since they play key roles as pollinators, herbivores and detritivores and act as a food source for numerous other organisms, e.g. for the high proportion of insectivorous mammals (Malcolm 1997). Due to their unparalleled diversity and overall ecological importance, changes of insect populations caused by responses to habitat modification are probably directly or indirectly affecting other ecosystem components (Malcolm 1997).

The best way for a better understanding of the mechanisms that generate and maintain tropical biodiversity may be a comprehensive overview of the local canopy fauna. Therefore, the canopy dwelling arthropod communities at different sites in the Kakamega Forest in Kenya have been collected using the insecticidal fogging technique, which allows besides quantitative assemblages also for the investigation of true abundances of arthropods. Since one of the aims of the BIOTA project is the

analysis of changes of biodiversity and ecosystem function along gradients of degradation (Köhler & Naumann 2003), the sites studied are along a gradient of disturbance, from nearly primary to secondary forest and adjacent forest fragments. As suggested by Floren & Linsenmair (2003) assemblages of disturbed forests should be clearly distinct from those of the primary forest, since anthropogenic disturbances have long-lasting effects on beetle diversity and assemblage structure, even after 40 years of regeneration of the secondary habitats.
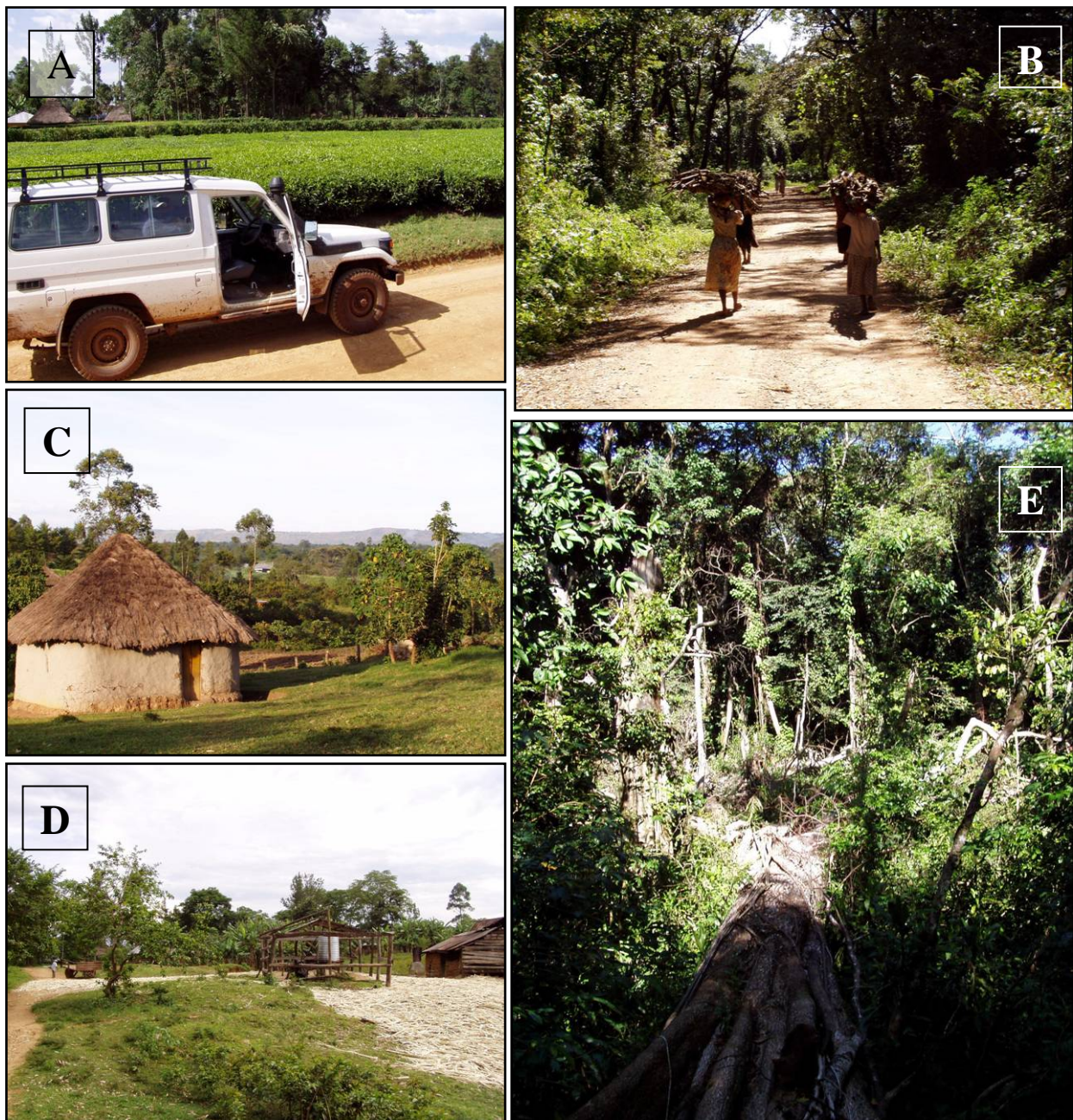
Fig. 1: Causes of deforestation: tea plantation in Isecheno (A); women collecting fire wood (B); expanding population and villages (C); processing of sugar cane which is planted around the forest (D); natural glade made by a fallen tree at the Colobus Trail (E).

Moreover, the distribution of beetles in tropical forests probably also depends on the structure and composition of the vegetation of the sites and on the forest type, respectively (Wagner 2000a). Therefore, also changes of the habitats by fragmentation and degradation should have affects on the diversity structure of the beetle communities. Comparisons of these communities between and within different forest types and the investigation of their distribution patterns should make clear to what extent these assumptions are true. In particular, phytophagous beetles like leaf beetles (Chrysomelidae) and weevils (Curculionidae) are excellent target groups due to their species richness and abundance as one of the dominant arthropod groups in tropical forests with a key position between plants and first order consumers. Analyzing influences of man-made changes, degradation and fragmentation of forest habitats on the diversity of these beetle communities and to which extent species assemblages are influenced by seasonality, structure and geographical distance of fragments are main aims of this study. This work was meant to uncover some possible patterns which enable for the coexistence of beetle communities, but is certainly only able to illuminate a very small fraction of the complex correlations within a tropical rain forest.

Since two different tree species were investigated, some statements also on specialisation of phytophagous insects could be studied, which is a key position for the understanding of tropical biodiversity (Lawton & Strong 1981, Gaston 1991b, Price et al. 1995). There are indications for some taxa that the proportions of generalists are higher in the tropics than in temperate regions (Beaver 1979a, b, Price 1991). This fact would fit the stochastic non-equilibrium model which also implicates higher niche overlap of species and low specialisation. Which model (stochasticity versus deterministic equilibrium model) is more likely for the distribution patterns of arthropod communities in Kakamega Forest, also could be studied.

2. Material and methods

2.1. Study time and area

The field work was conducted at five different sites in the Kakamega Forest, a tropical rain forest in Kenya, two times during the wet season in September and October 2001 and 2002 and again two times during the dry season in January 2002 and 2003.

Kakamega Forest

Kakamega Forest is generally considered to be the eastern-most remnant of the lowland guineo-congolian rain forest belt (Kokwaro 1988), formerly represented as a complete forest area from Western Africa throughout the Congo Basin towards Eastern Africa. Thus, it is the only remnant in Kenya of rain forest dwelling animals and plants, but due to its elevation it also contains montane elements of flora and fauna (Althof et al. 2003). These species are threatened by the great pressures of harvesting and forest exploitation. Kakamega Forest is severely overexploited due to its small size and dense surrounding population. It is located amidst the densest populated agricultural centre in the world with about 600 people per km^2 (Blackett 1994, Tattersfield et al. 2001) and with a population growth rate in 1990 of 3.8 % (Rodgers 1992), an increase of population density in the next decades is most likely (Cincotta et al. 2000). This would intensify the anthropogenic impact on the forest even more and the conflict between nature conservation and land use would increase at the same time (Balmford et al. 2001).

Over 20 % of the forest was lost in the last 30 years (KIFCON 1994, Lung & Schaab 2004). The forested area is not only reduced, but it is being fragmented into islands of indigenous growth separated by clear cuts and exotic forest plantations. Bennun & Njoroge (1999) estimated only some 12,000 ha of forest and also a current measuring based on a Landsat 7 imagery from 2001 revealed remains of 12,200 ha of wooded area (Lung & Schaab 2004). Apart from the main forest area there are two isolated fragments in the north, namely Malawa and Kisere, and three in the south, Yala, Ikuywa and Kaimosi (Brooks et al. 1999). About 4000 ha of the northern Buyangu part of the forest and the Kisere Forest are declared as National Reserves under management of the Kenya Wildlife Service (KWS) with conservation of biodiversity as their main dogma (KIFCON 1994). The larger southern Isecheno part is under the administration of the Forest Department (FD).

Geography and climate

Kakamega Forest is situated in the Shinyalu Division of Kakamega District in the Western Province of Kenya. It lies north-east of the Lake Victoria between latitudes of

00°10'N and 00°21'N and longitudes of 34°47'E and 34°58'E at about 1600 m above sea level (Fig. 2, left). The forest area is drained by two main river systems, the Isiukhu River to the north and the Yala River to the south (Fig. 4, A). Along its eastern edge rises the merely partially forested Nandi Escarpment with elevations up to 2200 m which runs along the western edge of the Great Rift Valley. South of the escarpment the Southern Nandi Hills are situated (Fig. 2, right).
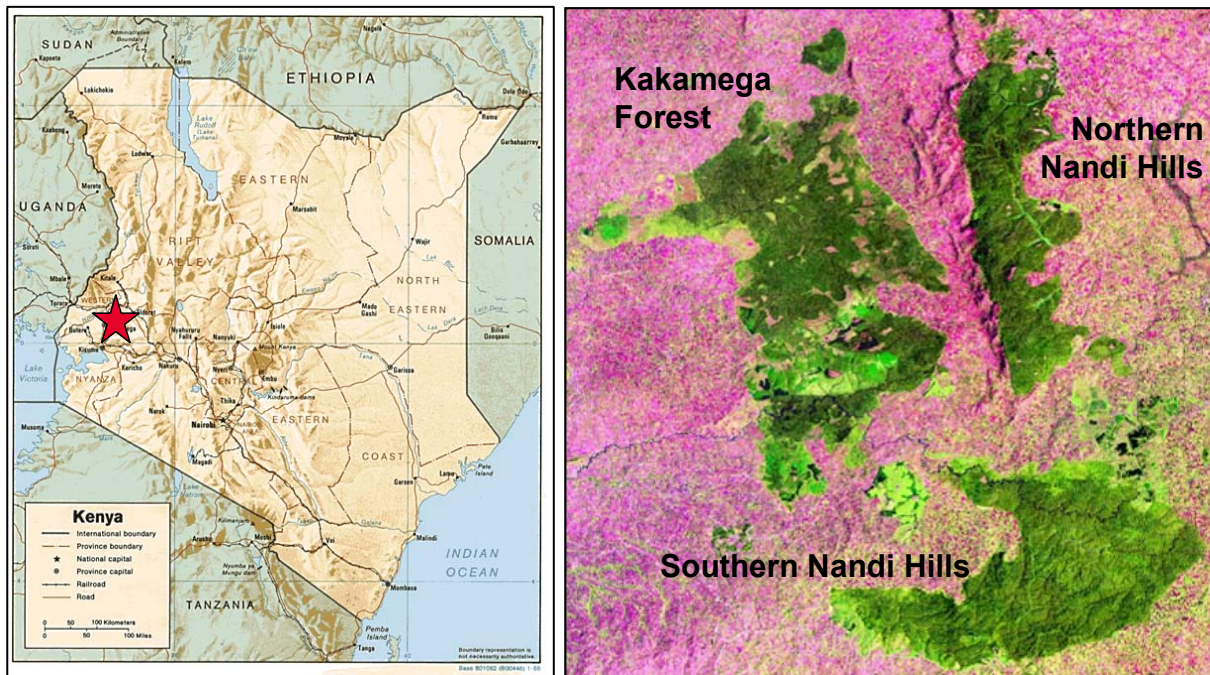
Fig. 2: Position of the Kakamega Forest in Western Kenya (left, red marker) and a satellite image of the forested areas next to the Nandi Escarpment and the Southern Nandi Hills (right) (Landsat, BIOTA E02, G. Schaab).

Mean annual precipitation is 2147 mm (1959−1985 Kakamega Town, Tsingalia 1988), concentrated in two wet seasons, first in April and May ("long rains") and second in September and October ("short rains", see Fig. 3). The dry season is from the end of December to February, with January as the driest month, but during the field work even heavy rains occurred from time to time. In contrast to temperate zones the temperature is fairly constant throughout the year, with mean daily minimums of about 15°C and daily maximums from 21°C to about 26°C (KIFCON 1994), known as daytime climate (Fig. 3).

Main forest areas and fragments studied

In Kakamega Forest, about 320 species of vascular plants and several different types of plant communities can be found (Althof et al. 2003). This mosaic of different vegetation types is probably a result of human impact (Althof et al. 2003). A typical primary forest

cannot be found. In addition to areas classified as "primary-like" rain forest, there are other types like colonizing forest, disturbed forest, clearings and natural glades, plantation areas and riverine forest. Three of the five study sites are located within the main forest, namely along the Colobus (Mukhangu) Trail, along the Isiukhu River and at the Busambuli River Trail. Two isolated fragments have been investigated, Kisere to the north and Yala to the south (Fig. 4, A). Due to the varying vegetation of Kakamega Forest a general description of the dominating species of the upper canopy layer (15−30 m), middle canopy layer (5−15 m) and understorey (1−5 m) can be hardly given and therefore it is presented in detail for each site including the definition of the forest type (all data from Althof, unpublished, BIOTA E04).
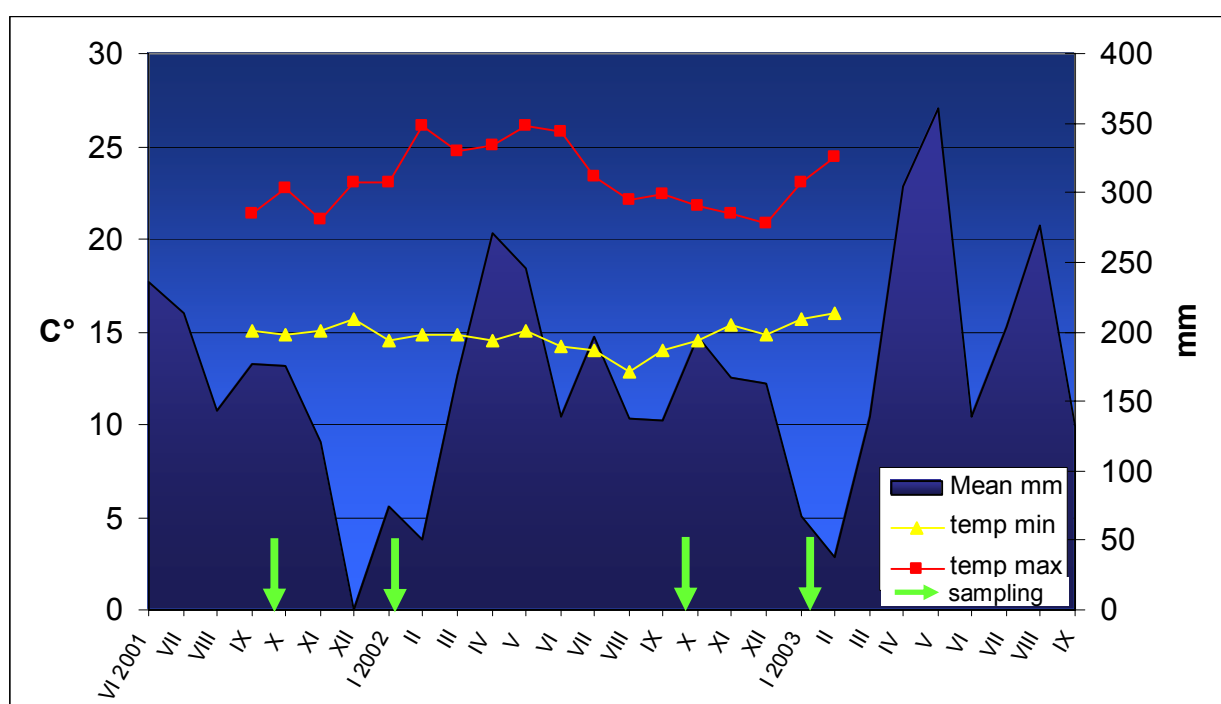
Fig. 3: Mean annual rainfall (mm), mean maximum and minimum daily temperature (°C) and time of fogging events (green marker) in Kakamega Forest from June 2001 to May 2003 (Datalogger, BIOTA E02; Isecheno forest station).

The Colobus Trail is situated in the very north of the main forest and is nowadays a relatively undisturbed and very well protected area (Fig. 4, A). It is an old secondary forest with an advanced, regenerating vegetation which is about 30−50 years old. The upper canopy layer is dominated by *Antiaris toxicaria*, *Celtis africana* and *Polyscias fulva*, the middle canopy layer by *Celtis africana*, *Heinsenia diervilleoides*, *Strychnos usambarensis*, *Teclea nobilis*, *Trichilia ernetica* and *Trilepsium madagascariense*. In the understorey *Coffea eugenioides*, *Dovyalis macrocalyx*, *Dracaena fragrans* and *Heinsenia diervilleoides* can be found as abundant tree species. The forest along the Isiukhu River is about four kilometres away from the Colobus Trail separated by open

grassland (Fig. 4, B). It is a middle-aged secondary forest with *Celtis africana*, *Polyscias fulva* and *Prunus africana* in the upper canopy layer, which reaches a height of only 10−20 m. Many species in the middle canopy layer like *Blighia unijugata*, *Chrysophyllum albidum*, *Harungana madagascariensis*, *Maesa lanceolata*, *Oncoba spinosa* and *Teclea nobilis* show the intermediary type of this site, which is about 20−30 years old. But there are also many patches with young secondary forest, about 10−20 years old. The understorey consists of many different species (e.g. *Acanthus eminens*,
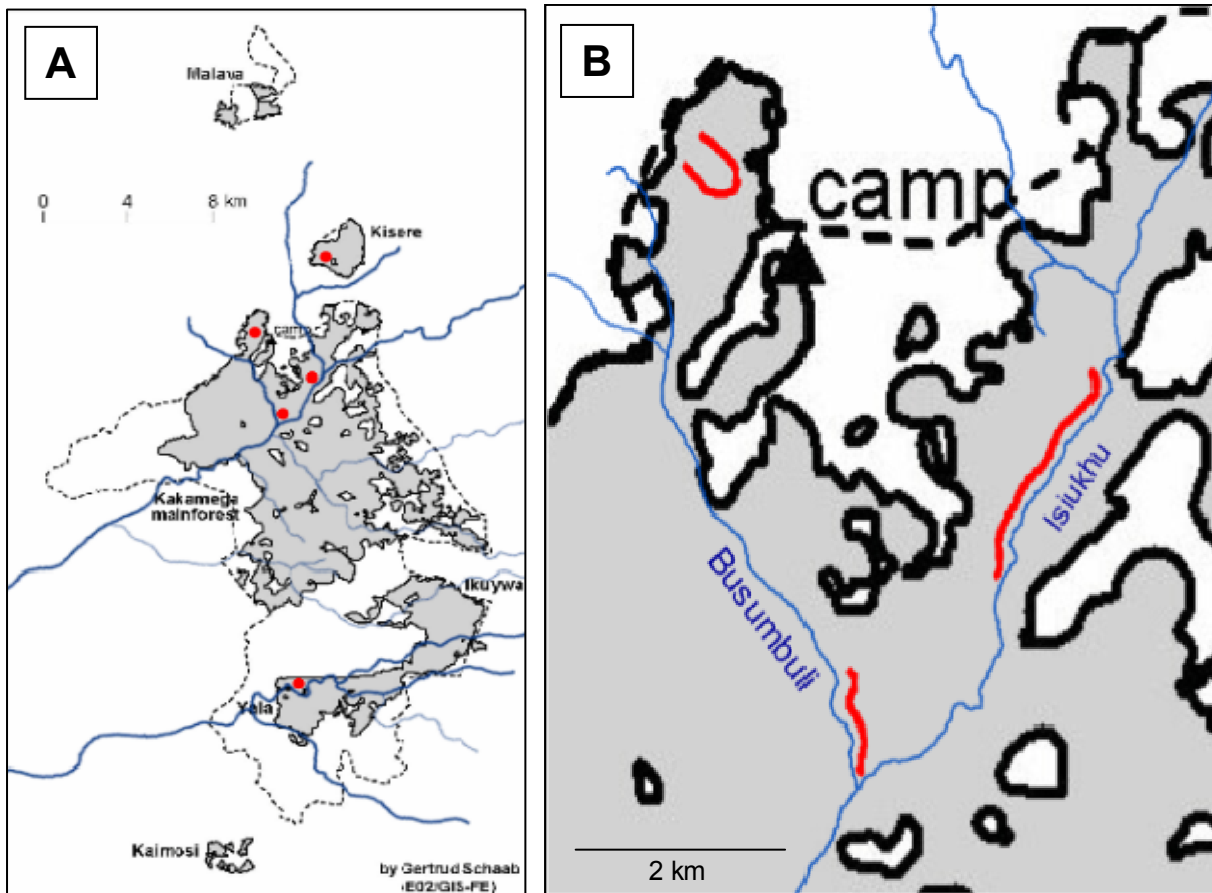
Fig. 4: (A) Schematic view of Kakamega Forest and position of study sites (red dots), wooded area (grey) and forest boundaries (dashed line); (B) close up of the transects (red line) at the Colobus Trail, Isiukhu River and Busambuli River (map from G. Schaab BIOTA E02, river system added).

Allophylus ferrugineus, Blighia unijugata, Coffea eugenioides, Diospyros abyssinica, Dracaena fragrans, Funtumia africana, Heinsenia diervilleoides, Oncoba spinosa and *Teclea nobilis*) and many pioneer species. It is more open than the others and because of the close distance to the river this area is very wet and most of the tree trunks were overgrown with moss. While the sites at Colobus trail and Isiukhu River are only connected with the main forest through a small corridor of native wood to the south and fragmentation was at least in progress, the plot at the Busambuli River is situated within the main forest with connections in all directions. It is an intermediary, middle-aged

secondary forest. More species in the lower stratum show that the forest is regenerating since 20−30 years. These species are *Celtis mildbraedi* and *Teclea nobilis* in the middle canopy layer and *Funtumia africana*, *Heinsenia diervilleoides*, *Teclea nobilis* and *Rinorea brachypetala* in the understorey. *Dracaena fragrans* is also very abundant. The upper canopy (up to 25 m) is dominated by *Celtis gomphophylla, Celtis mildbraedi* and *Croton megalocarpus*. These three study sites build a triangle, whereat the distance of fogged trees is lower between Busambuli and Isiukhu River (Fig. 4, B).
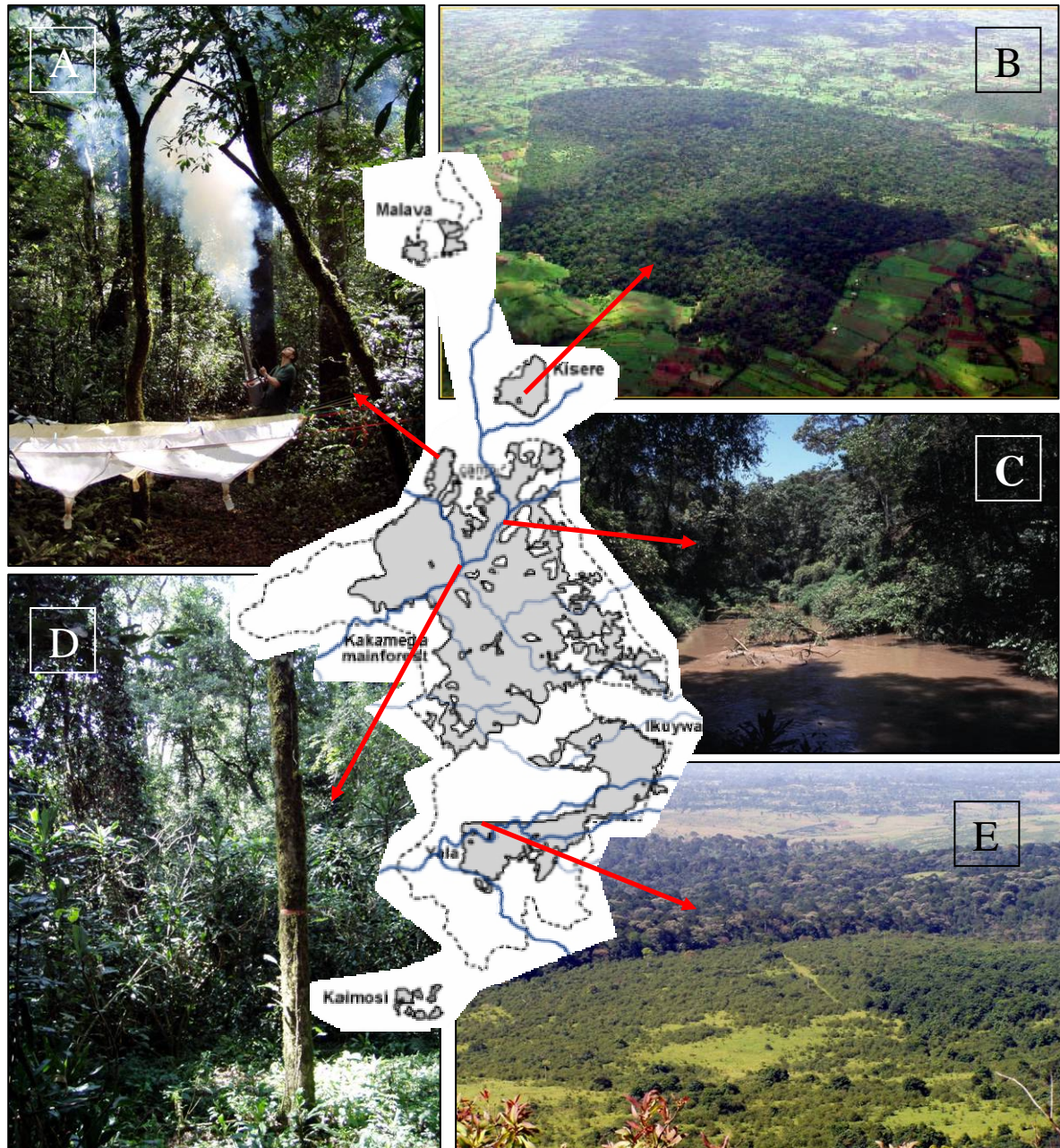
Fig. 5: (A) Fogging a tree at the Colobus Trail; (B) aerial view of the Kisere Forest (picture from BIOTA E02); (C) the Isiukhu River; (D) fogged tree at the Busambuli River Trail; (E) aerial view on the Yala fragment with grassland and guava plantation in foreground (looking southward).

Kisere Forest has been isolated for at least 70 years, but it is thought to be nearly primary and undisturbed for more than 50 years and therefore one of the oldest parts of the entire forest. This can be derived from the amount of tree species in the upper canopy which is up to 30 m high, e.g. *Aningeria altissima*, *Antiaris toxicaria*, *Celtis africana, Diospyros abyssinica, Funtumia africana, Olea capensis* and *Strychnos usambarensis*. The dominating species of the middle canopy layer are *Blighia unijugata* and *Heinsenia diervilleoides*. In the understorey *Allophylus ferrugineus, Bequaertiodendron oblanceolatum, Cassipourea ruwensorensis, Coffea eugenioides, Dovyalis macrocalyx*, *Dracaena fragrans, Funtumia africana, Heinsenia diervilleoides, Rawsonia lucida* and *Uvariopsis congensis* are growing, indicating that Kisere Forest is still regenerating. Nevertheless, fogging was conducted in the northern, more disturbed part of the fragment. The distance to the next forest area is 1.6 km, it is about 420 ha in size and surrounded by plantations of maize and sugar cane (Fig. 4 A, Fig. 5 B). The Yala forest section is thought to have been isolated for more than 30 years from the main forest and in latest history also from Ikuywa (G. Schaab pers. comm.). The gap to the main forest is about 4 km in size and it consists of grassland, planted with exotic guava (*Psidium guajava*). These plantations maybe serve some forest dwelling species as "stepping stones" and they probably counteract the isolation from the main forest (Fig. 4 A, Fig. 5 E). The fragment is about 1180 ha in size and consists of an advanced secondary forest which is nearly 30−50 years old and up to 25 m high. The dominating species of the upper canopy are *Antiaris toxicaria*, *Casaeria battiscombei*, *Celtis mildbraedi, Croton megalocarpus* and *Funtumia africana*. In the middle canopy layer *Blighia unijugata, Craibia brownie, Craterispermum schweinfurthii* and *Trilepsium madagascariense* and in the understorey *Acalypha* spec., *Allophylus ferrugineus, Dracaena fragrans, Funtumia africana* and *Heinsenia diervilleoides* are dominating. The distance to the next study site (at the Busambuli River Trail) is about 15 km.

2.2. Canopy dwelling arthropods collected by insecticidal tree fogging

Investigations on arboricolous arthropods were up to now the focus of ecological studies. First approaches on this topic were conducted with insecticide-spray techniques and with the improvement of other canopy access techniques such as walkways, cranes, canopy rafts and insecticide fogging, the work on canopy dwelling arthropod communities rapidly increased (Mitchell 1982, Lowman et al. 1993, Moffett

1993, Basset et al. 1997, Stork & Hammond 1997, Barker & Pinard 2001). Since canopy fogging was introduced as a 'new' method for field work at the end of the 1970's (Sutton 2001), this type of research has become very effective and nowadays one can scarcely imagine canopy research without the fogging technique. With this method an insecticide with a carrier is brought out as a fog with a so called swingfog machine, originally introduced for pest control in greenhouses, which employs the active agent much more efficiently than the spray method. Only this method allows quantitative assemblages and true abundances of most of the arthropod groups (Basset et al. 1997, Sutton 2001, Wagner 2001). Using the appropriate insecticide dose, arthropods are only knocked down for a while and still can be used for auto-ecological experiments and studies on their biology after recovering (Paarmann & Stork 1987, Paarmann 1994, Adis et al. 1997, Paarmann & Kerck 1997, Paarmann & Paarmann 1997).

2.2.1. Sampling procedure

Canopy fogging of each tree was carried out from the ground using an SN50 Swingfog insecticide fogger (Fig. 6 A). The insecticide used was a non-residual natural Pyrethrum extract (25 %), which is decomposed in sunlight and only harmful to invertebrates (Stork 1991, Casida & Quistad 1995, Floren & Linsenmair 2001). It is derived from the dried flowers of the plant *Chrysanthemum cinerariaefolium* (Asteraceae) and Kenya is one of the main producers of pyrethrum in the world (Fig. 6 B). The name given to the active insecticidal components of the dried flowers is pyrethrins (Casida & Quistad 1995). In order to make the fog visible, diesel oil was used as a carrier for the knockdown-insecticide, with a concentration of 1.5 % active ingredient. Fogging was carried out on days with calm wind and dry weather conditions. Windless conditions are required to allow the hot fog to rise up through the canopy and to collect the knocked-down insects without drifting outside the range of the collecting sheets, which roughly reflect the crown size. Dry canopy and weather conditions are important to prevent the risk of insects sticking on wet leaves in the canopy or on the wet sampling sheets. Samples were collected in 16 funnel-shaped sheets, each of 1 m² size, made of smooth nylon. The sheets were suspended from a network of ropes at about one meter height (Fig. 6 C). After about five minutes sufficient insecticide was released to the entire canopy and smaller arthropods immediately fell down. After a drop time of 90 minutes sheets were gently brushed so that the trapped insects drop into the collecting jars which are suspended in the centre of the sheets. Finally, material from each tree was preserved in 98 % Ethanol.
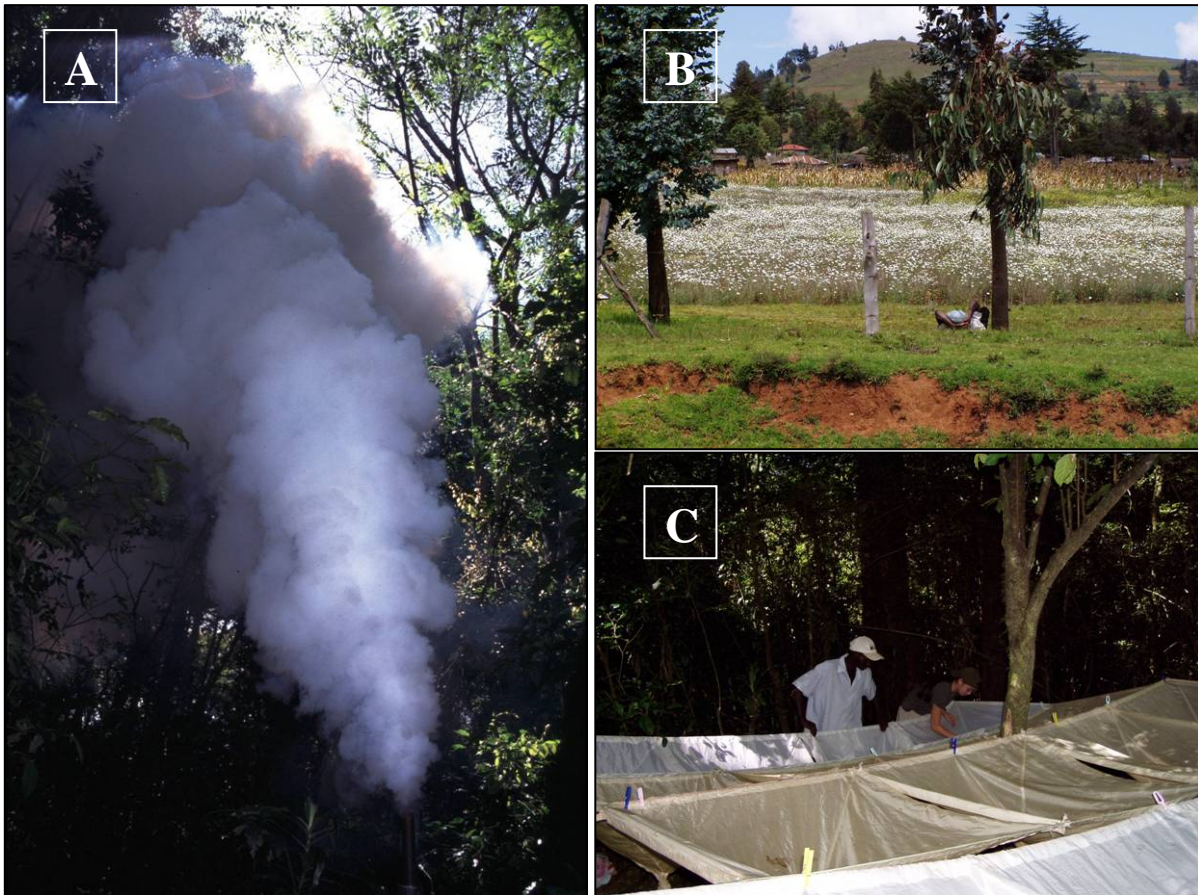
Fig. 6: (A): the hot fog rises through the canopy of a selected tree; (B): the white flower of *Chrysanthemum cinerariaefolium* (Asteraceae) growing in a plantation near Kericho; (C): suspended sampling sheets beneath the canopy of the tree investigated.

2.2.2. Trees investigated

On each study site a group of eight conspecific trees, subsequently named 'collecting unit', was fogged. The investigated tree species at the Colobus Trail, Isiukhu River, Busambuli River and Yala River was *Teclea nobilis* Delile (Rutaceae). It is an evergreen tree, 4−18 m high, with 3-foliated leaves (Fig. 7 A). Since no suitable trees of this species could be found in Kisere (tree heights only less than four or more than 16 meters), a further tree species, namely *Heinsenia diervilleoides* K. Schum. (Rubiaceae), has been studied. It is also an evergreen tree, from 2−9 m in height and with 1-foliated leaves (Fig. 7 B). To make this collecting unit comparable to the other sites another eight trees of this species were also fogged at the Colobus Trail (Table 1). Both tree species are among the commonest species of the lower and middle canopy of the forest and are used by the local people for firewood and the roots also for walking sticks. Historical data show that *Teclea nobilis* was logged only in the 1950's (20,920 m³) and no more records of logging exist after 1958 (Mutangah et al. 1992).

The canopy of the selected trees should be isolated from other canopies as far as possible to ensure that the arthropods collected can reasonably be expected to have been associated with the fogged tree. The tree top should not exceed a total height of 13 meters to ensure that the fog rises up through its complete height. In other works (Erwin & Scott 1980, Erwin 1983, Adis et al. 1984, Stork 1987b, a, Morse et al. 1988, Hammond 1990, Stork & Brendell 1990, Basset & Kitching 1991, Allison et al. 1993, Kitching & Arthur 1993, Floren & Linsenmair 1994) trees with heights up to 72 m (Stork 1988) have been investigated. Working on those trees with a height of more than 13 meters is only practicable with a rope and pulley system, since the risk of drifting fog rises with tree height. On the other hand, also the risk of drifting of the dropping insects increases and very small, soft bodied arthropods, mainly Thysanoptera and tiny Hymenoptera, are certainly under represented in such assemblages. Furthermore, high mobile insects are probably disturbed during the installation of the fogger. Starting in the very early morning hours when no wind occurs was also not practicable, since the leaves were still wet from the rain or dew at night, even during the dry season. Therefore, work usually started around 9 to 10 a.m. A dry canopy was important to avoid smaller and soft bodied insects from sticking onto leaves or wet sheets. The trees should neither be flowering nor fruiting to minimize the portion of flower and fruit visitors. Furthermore, the trees should stand isolated, as far as possible, and should not be overgrown with climbers.
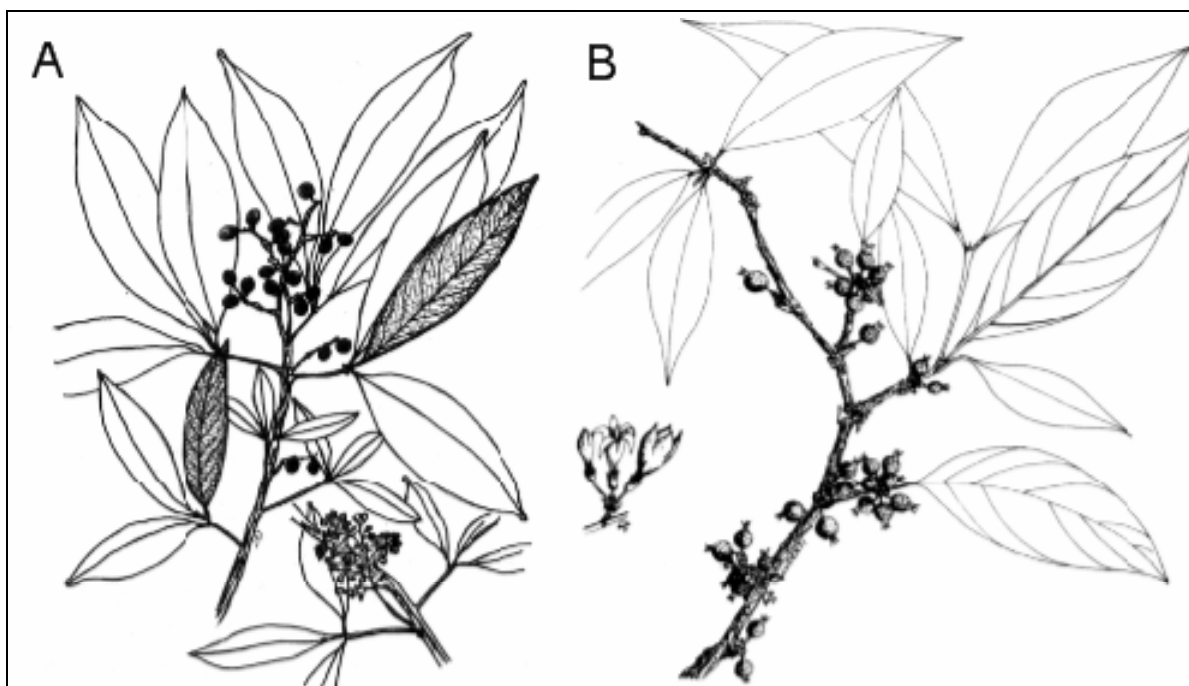
Fig. 7: Studied tree species; (A) *Teclea nobilis* Delile (Rutaceae) and (B) *Heinsenia diervilleoides* K. Schum. (Rubiaceae) (from Beentje 1994).

Exploited canopy volumes were measured by calculating the radius and height of the canopy (in m) and estimating the density of leaf cover (in %) multiplied by 16 (area of collecting sheets). This leads to a standardized sampling regime, which allows a clear comparison of the arthropod assemblages from the study sites in the main forest and in the fragments. Chance effects can be reduced and the results can be effectively tested statistically.

Table 1: Over view of trees examined. The abbreviations are subsequently used in graphs, tables and figures.

sample site		tree species	exploited canopy volume (m³)	abbreviation
Busambuli River	main forest	*Teclea nobilis*	296,4	**bus**
Isiukhu River	main forest	*Teclea nobilis*	300,0	**isi**
Yala River	forest fragment	*Teclea nobilis*	281,2	**yal**
Colobus Trail	main forest	*Teclea nobilis*	317,2	**col**
Colobus Trail	main forest	*Heinsenia diervilleoides*	223,2	**hein**
Kisere Forest	forest fragment	*Heinsenia diervilleoides*	238,8	**kis**

The selected tree species are systematically not closely related. If beetles, and in particular the phytophagous beetles, are restricted to one host tree, a possible impact of the tree species on the diversity structure of the beetles should be recognized in the faunal overlap within and between tree species, since similarities of insect assemblages decrease as the inter-tree taxonomic distance increases (Kitching et al. 2003).

2.2.3. Efficiency of the fogging technique

Pyrethrum is a very effective contact insecticide attacking the nervous system of insects almost immediately and causing uncontrolled movement and finally knockdown (Elliott et al. 1978). Even weevils and leaf beetles, which are highly adapted on smooth surfaces, are no longer able to stay on the leaves and fall down. This work was done without examination of sawed branches after fogging (e.g. Allison et al. 1993) or shaking of the trees, because additional experiments like these normally do not reveal more beetles, but only more ants, which still come out of their nest after fogging. Moreover, by shaking trees the portion of moss, small twigs and leaves increases and this would raises difficulties in sorting the sampled arthropods. It was also refrained from wrapping the entire canopy to prevent highly mobile insects like dragonflies and some Hymenoptera and Diptera from escaping the fog, because of the probable arising

disturbance to the arthropod communities such activity would create, and the high logistic expenditure in the forest.

There are a number of advantages of the fogging technique: e.g. no attractants are involved, it is not influenced by trap behaviour, there is no need to climb or disturb trees, it is not dependant on the activity of the canopy dwelling arthropods and they can be quantitatively collected (Stork & Hammond 1997). This technique allows quantitative assemblages of arthropods, which are living on leaves, twigs and trunks of the investigated trees or are flying in their canopies. Phloem-feeders like aphids and scale insects, which do not pull out their mouthparts and "get stuck" in the plant tissue, and arthropods, which are mostly living in the wood or under the bark (e.g. wood borer), are collected more by chance. Miners, gall forming organisms and termites are never caught with this method. Nevertheless, this technique is more suited for a quantitative survey of most taxa present than any other sampling method.

2.3. Evaluation of fogging experiments

2.3.1. Sample sorting

After returning from Kenya the sampled arthropods were sorted to major groups and counted. Larvae and specimens were partly identified using Stehr (1987, 1991) and CSIRO (1991a, 1991b), which is also helpful for samples of the African insect fauna. Very small and frequently found insects like springtails and thrips have been counted partly and their total abundance in the entire sample was calculated on basis of a random sample.

2.3.2. Beetle morpho-types and beetle species

Besides numbers of specimens of course species numbers are necessary when working on biodiversity. Since alpha-taxonomy of most tropical insect groups is still very incomplete and the portion of undescribed species is very high, identification to species of the entire material is impossible. Taxonomic work would require much time for the generation of revisions, provided that specialists for the several groups exist. Nevertheless, if comparisons of diversity should be done, the collected material needs to be allocated to morpho-types. This method is quite a good approach comparable to actual species numbers (Hammond 1994, Wagner 1996).

Beetles were chosen owing to their high species number, which allows best statements about diversity of the studied sites. Moreover, to yield accurate results by allocation to morpho-types it assumes good knowledge of the group and this was the case for beetles, especially for Chrysomelidae (e.g. Wagner 2000b, Middelhauve & Wagner 2001, Wagner & Scherz 2002, Freund & Wagner 2003, Wagner & Freund 2003). Generally this procedure leads more to lumping (more than one species classified as one morpho-type) than to splitting (one species separated into more than one morpho-type), because nonrecognition of sister species is more likely than overestimating polymorphisms (Derraik et al. 2002). Subsequently, the term of *morpho-types* is consequently replaced by the term of *species*.
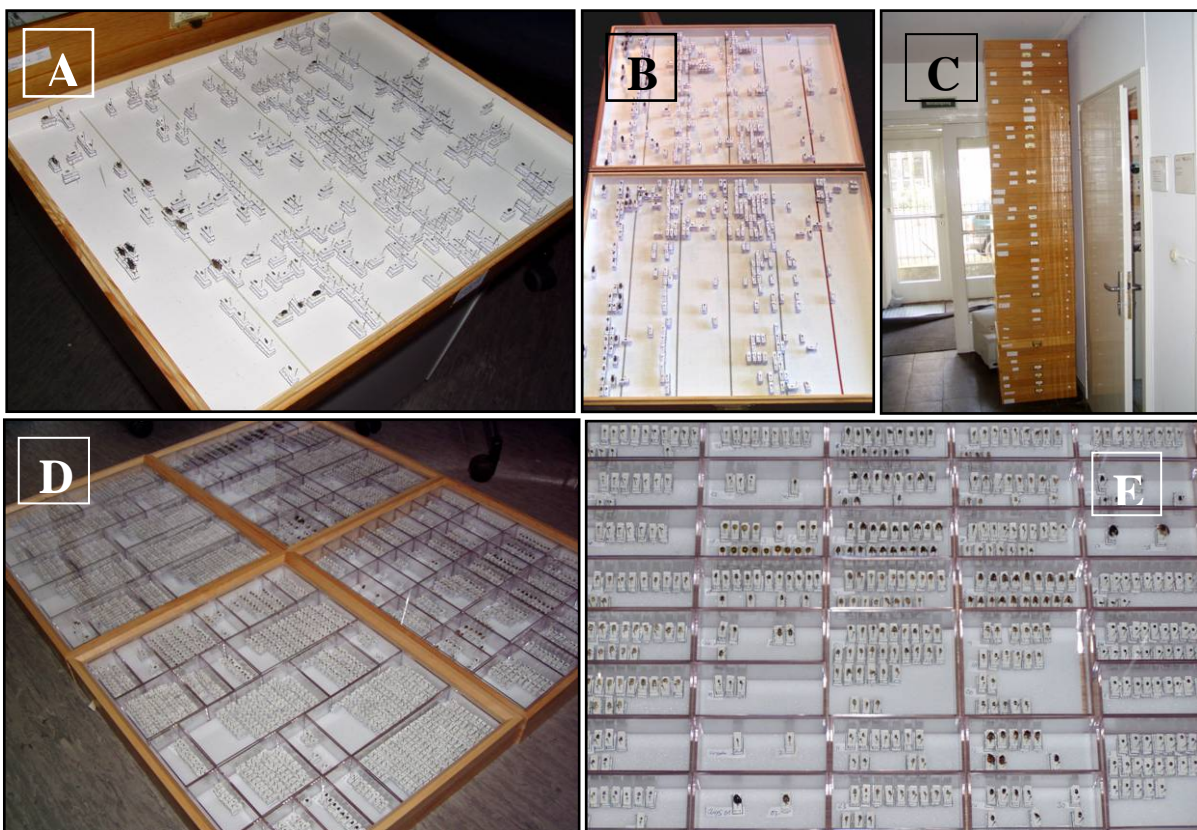
Fig. 8: Arrangement of species in rows (per tree) and columns (per morpho-types) for easier assessment and compilation of data (A-C) and the transfer of conspecific specimens into single boxes including a code-number (D, E).

At least one specimen of each beetle species of each tree was card-mounted or pinned and labelled. The above arrangement of insect boxes, showing the beetle species of one tree per row and same species one beneath the other in one column, was used for assessment and compilation of data (Fig. 8 A-C). Afterwards beetles were transferred into boxes, one for each species. This made the sampling more clearly arranged and the work on the collection easier (Fig. 8 D, E).

2.3.3. Allocation to feeding guilds

Though the leaf beetles were the focus of this project, also some other beetle groups were studied in detail. This allows a comparison between the ecological groups and a confirmation of the question by which factors (i.e. seasonality, forest type or host tree) these groups are influenced. The allocation of beetles to feeding guilds is mainly based on works of Crowson (1967), authors of Freude et al. (1964−1983), Jacobs & Renner (1988) and Lawrence & Britton (1991). As stressed by Hammond (1994), allocation of species to feeding guilds always involves possible errors. This applies especially for assemblages of tropical arthropods where for some species very little is known about their biology. Therefore, only those species that could be confidently assigned were allotted to the guilds. These guilds are phytophagous, mycetophagous and predacious beetles. Two phytophagous groups of beetles have been studied most intensively. The first group are Chrysomelidae, where adults and larvae feed on leaves and some of them remain on their host plants for their entire lifetime. Bruchinae which are mainly feed on seeds are excluded, despite being phylogenetically part of the Chrysomelidae (Reid 1995). The second group are the phytophagous weevils, namely Apionidae and Curculionidae (excluding the xylophagous Scolytinae and Platypodinae). Several species of this group are not able to fly and they have to move on the ground in order to reach the next food plant. Thus, the distribution of this group, as opposed to the Chrysomelidae, is affected by different factors, for instance the presence of rivers as boundaries. The mycetophagous beetles studied in detail are Mycetophagidae, Biphyllidae, Corylophidae, Cryptophagidae and Latridiidae and the group of predacious beetles consists of the carnivorous Staphylinidae (including Pselaphinae) and Carabidae. Since species which are living in the wood or under the bark are not effectively and only irregularly sampled with the fogging technique, xylophagous beetles were excluded from analysis. Because of the different way of life of the established guilds, they are probably influenced by different factors and their distribution patterns should also differ.

2.4. Diversity measures

For diversity estimates and the mathematical description of a biocoenosis, numbers of individuals and species are necessary. After allocating the material to morpho-types (see above) these numbers are now available for beetles. Hence, diversity measures are only calculated for this group and in particular for the feeding guilds investigated. To compare the samples of the study sites several indices and estimators were chosen. The variables that are used in the equations are shown and their definitions explained in

Table 2. Variables not listed in the table are explained separately in the respective formulas. The statistical estimation of species richness and shared species from samples was computed with EstimateS, Version 6.0b1 (Colwell 1997).

Table 2: Variables on species diversity used in the equations (from User's Guide Colwell 1997).

S_{obs}	Total number of species observed
S_{rare}	Number of rare species (each with 10 or fewer individuals)
S_{abund}	Number of abundant species (each with more than 10 individuals)
S_{infr}	Number of infrequent species (each found in 10 or fewer samples)
S_{freq}	Number of frequent species (each found in 10 or more samples)
m	Total number of samples
m_{infr}	Number of samples that have at least one infrequent species
F_i	Number of species that have exactly i individuals when all samples are pooled (F_1 is the frequency of singletons, i.e. number of species which occur only once in a single sample, F_2 the frequency of doubletons…)
Q_j	Number of species that occur in exactly j samples (Q_1 is the frequency of uniques, i.e. number of species which occur only once in all of the pooled samples, Q_2 of duplicates…)
N_{rare}	Total number of individuals of rare species
N_{infr}	Total number of incidences (occurrences) of infrequent species
C_{ace}	Sample abundance coverage estimator
C_{ice}	Sample incidence coverage estimator

2.4.1. Alpha-diversity

The idea of alpha- or species-diversity of a biocoenosis, in this work represented by the community of a single tree, generally contains two distinct concepts (Krebs 1999). The first and simplest concept is the number of species found, the species richness (McIntosh 1967). For its description lots of indices have been introduced, but the basic problem is that it is quite impossible to enumerate all species, in particular arthropods, in a natural community. The second concept of diversity, the heterogeneity, combines two separate ideas of species richness and evenness (Simpson 1949). The idea of evenness emphasizes the distribution of species in a community, based on the fact that most communities contain a few dominant species and many species are relatively uncommon. Evenness measures attempt to quantify this unequal distribution against a hypothetical community in which all species are equally common (Krebs 1999). To many ecologists heterogeneity is synonymous with "diversity" (Hurlbert 1971).

Number of species observed in the pooled samples: S_{obs}

Species numbers are a basic feature of diversity. For each collecting unit the observed number of species (pooled) is given. The equation is

$$S_{obs} = S_{rare} + S_{abund} \ .$$

Coverage-Based Richness Estimators: ICE and ACE

Since it is quite impossible to sample all species in a given community of insects the total species richness can only be estimated. The two relatively new introduced estimators, ICE (Incidence-based Coverage Estimator) and ACE (Abundance-based Coverage Estimator) are modifications of the Chao and Lee estimators (Chao & Lee 1992) discussed by Collwell and Coddington (1994). They are based on the statistical concept of sample coverage from Chao and Lee (Chao & Lee 1992, Chazdon et al. 1998, for details see Colwell 1997). These estimators are modified coverage-based estimators for both abundance data and incidence data to overcome the problem of overestimating species richness. That is a characteristic problem of assemblages of tropical arthropods in which some species are very common and others very rare (Peterson & Slade 1998). Recognizing that all the useful information about undiscovered species lies in the rarer discovered species (Colwell 1997), the Abundance-based Coverage Estimator is based on those species with 10 or fewer individuals in the sample (Chao et al. 1993). The corresponding Incidence-based Coverage Estimator, likewise, is based on species found in 10 or fewer sampling units (Lee & Chao 1994).

ACE: Abundance-based Coverage Estimator of species richness (Chao & Lee 1992, Chao et al. 1993). The sample coverage estimate based on abundance data is

$$C_{ace} = 1 - \frac{F_1}{N_{rare}} \quad , \text{ where } \quad N_{rare} = \sum_{i=1}^{10} i F_i \ .$$

Thus, this sample coverage estimate is the proportion of all individuals of rare species that are not singletons (i.e. number of species which occur only once in a single sample). Then the ACE estimator of species richness is

$$S_{ace} = S_{abund} + \frac{S_{rare}}{C_{ace}} + \frac{F_1}{C_{ace}} \gamma^2_{ace} ,$$

where γ_{ace}^2, which estimates the coefficient of variation of the F_i's, is

$$\gamma_{ace}^2 = \max\left[\frac{S_{rare}}{C_{ace}} \frac{\sum_{i=1}^{10} i(i-1)F_i}{(N_{rare})(N_{rare}-1)} - 1{,}0\right].$$

ICE: Incidence-based Coverage Estimator of species richness (Lee & Chao 1994). First note that

$$S_{obs} = S_{\inf r} + S_{freq}.$$

The sample coverage estimate based on incidence data is

$$C_{ice} = 1 - \frac{Q_1}{N_{\inf r}} \quad, \text{ where } \quad N_{\inf r} = \sum_{j=1}^{10} jQ_j.$$

Thus, the sample coverage estimate is the proportion of all individuals in infrequent species that are not uniques (i.e. number of species which occur only once in all of the pooled samples). Then the ICE estimator of species richness is

$$S_{ice} = S_{freq} + \frac{S_{\inf r}}{C_{ice}} + \frac{Q_1}{C_{ice}}\gamma_{ice}^2,$$

where γ_{ice}^2, which estimates the coefficient of variation of the Q_j's, is

$$\gamma_{ice}^2 = \max\left[\frac{S_{\inf r}}{C_{ice}} \frac{m_{\inf r}}{(m_{\inf r-1})} \frac{\sum_{j=1}^{10} j(j-1)Q_j}{(N_{\inf r})^2} - 1{,}0\right].$$

Abundance-based richness estimator: Chao 1

This is a very frequently used abundance-based estimator of species richness and therefore suitable to compare the presented results with those of other studies, for details see Chao (1984). The full, bias-corrected formula is

$$S_{Chao1} = S_{obs} + \frac{F_1^2}{2(F_2+1)} - \frac{F_1 F_2}{2(F_2+1)^2}.$$

Simpson's Index of diversity

Simpson (1949) introduced a nonparametric measure of diversity ranging from 0 (high diversity) to almost 1 (low diversity). The less a single species is dominant, the smaller becomes the value and the sample is supposed to be more divers. It was modified by Pielou (1969) for finite populations and suggested that diversity was inversely related to the probability that two individuals picked at random belong to the same species. The index used was

$$D = \sum_{i=1}^{s} \left[\frac{n_i(n_i - 1)}{N(N-1)} \right] \quad ,$$

where D = Simpson's diversity index
n_i = Number of individuals of species i in the sample
N = Total number of individuals in the sample = $\sum n_i$
s = Number of species in the sample.

Shannon's Index of evenness

If all individuals of a community are equally distributed among the species, it is supposed to be more diverse than a community with high dominance of single species. The index theoretically ranges from 0, if all individuals belong to one species, to 1, if all species are equally distributed among the species found. The index is derived from the Shannon index of diversity H' (Shannon & Weaver 1949, Hayek & Buzas 1996). Thus

$$J' = \frac{H'}{\ln(S)} = \frac{-\sum_i p_i \ln p_i}{\ln(S)} \quad , \text{ where } \quad H' = -\sum_{i=1}^{s}(p_i)(\ln p_i)$$

and J' = Shannon's index of evenness (calculated with base e logs)
H' = Shannon-Wiener index of species diversity (calculated with base e logs)
p_i = Proportion of total sample belonging to i th species.

Rarefaction

Generally, all diversity indices are highly dependent on the number of random samples. But the comparison of communities of different samples sizes is only allowed to a limited degree (Magurran 1988, Achtziger et al. 1992, Krebs 1999). The rarefaction method provides a measure of species diversity which is robust to sample size effects (Sanders 1968). It calculates the expected species numbers for all samples for a rarefied number of individuals, i.e. usually the number of individuals of the smallest random sample. This permits the comparison between communities where numbers and densities of individuals are very different, provided that samples are taxonomically similar (Simberloff 1979), as well as sampling methods (Sanders 1968). The calculated

rarefaction curves are well interpretable, since the end of these curves show the number of species and individuals collected and steeper curves indicate more diverse communities (Hurlbert 1971, Simberloff 1979). The equation is

$$E(\hat{S}_n) = \sum_{i=1}^{s} \left[1 - \frac{\left(\dfrac{N - N_i}{n} \right)}{\left(\dfrac{N}{n} \right)} \right]$$

where $E(\hat{S}_n)$ = expected number of species in a random sample of n individuals

      S = total number of species in the entire collection

      N_i = number of individuals in species i

      N = total number of individuals in collection = $\sum N_i$

      n = value of sample size (number of individuals) chosen for standardization
        ($n \leq N$)

      $\left(\dfrac{N}{n} \right)$ = number of combinations of n individuals that can be chosen from a set of

        N individuals (= $N!/n!(N-n)!$).

2.4.2. Beta-diversity

Comparisons of species diversity of neighbouring habitats, in this case the trees within and between the sampling sites, give data on the beta-diversity of the communities studied. One way to do this is to measure the niche overlap among different populations and to compare it with that of another one. The easiest way to measure the beta diversity of pairs of sites is by the use of similarity coefficients. Very useful and simple indices like Jaccard and Sørenson compare the number of species exclusively found in both samples. A great disadvantage of these calculations is that species abundance is ignored (Magurran 1988). Each species contributes with the same value irrespective if it is abundant or rare. Hence, these presence-absence based indices have been neglected and a quantitative data based similarity index was used.

Simplified Morisita Index of Similarity

This measure was first proposed by Morisita (1959) and simplified by Horn (1966) and therefore sometimes called Morisita-Horn Index. It is nearly independent of sample size, considers also species abundance and was even recommended as the best measure of similarity for ecological use by Wolda (1981). The index ranges from 0 (no species in common) to about 1 (complete similarity). It is calculated as

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

where C_H = Morisita-Horn Index

X_{ij}, X_{ik} = Number of individuals of species i in sample j and sample k

$N_j = \sum Xij$ = Total number of individuals in sample j.

2.5. Statistical approach and multivariate analysis

2.5.1. Statistics

A statistical survey is generally only useful with a random sample size of a minimum of eight (Sachs 1992). Since eight trees at every study site were investigated, these requirements were met for comparisons within one site, while the statistical evaluation for each arthropod group between the study sites was based on 48 random samples and on 192 between seasons, respectively. If means of assemblages differ significantly, this was tested by an Analysis of variance (one-way ANOVA), assuming that the response has a normal distribution. Multiple means comparisons were used to test which means (e.g. of which study site) are different from which other. To compare differences among the means of all sites, a post hoc test, namely the Tukey-Kramer HSD (honestly significant difference) test, was used. Differences between dry and wet season were compared pair wise using Student's t-test. The evaluation of abundances between arthropod groups was done by regression analyses. A significance probability less than $p < 0.05$ was interpreted as evidence that differences between groups or samples are significant, additionally intervals of $p < 0.01$ and $p < 0.001$ were given. Statistical calculations were calculated with SPSS 10.07, SPSS Inc. 1989−1999.

2.5.2. Multivariate analysis

The n-dimensions of all independent variables and data used in analyses make a graphical representation quite intricate and impossible, respectively. Therefore, the object is to describe a matrix of data by reducing the dimensions. In this case similar distributed variables are arranged and summarized by the multivariate methods. These are powerful descriptive methods which can suggest correlations between hidden biodiversity patterns and potential causes, but cannot resolve cause and effect (James

& McCulloch 1990). They were calculated with BioDiversity Pro, McAleece, NHM & SAMS 1997.

Jaccard-Cluster Analysis (Single Average Link)

A clustering method is a way to achieve a classification of a series of samples. Average Link clustering appears to give a useful hierarchy of clusters and it avoids the extremes introduced by single linkage and complete linkage clustering. Single linkage clustering tends to produce long, strung-out clusters while complete linkage clustering tends to the opposite extreme, producing very tight, compact clusters (Krebs 1999). The output shows a dendrogram showing the similarity between a sample and an existing cluster, which is by definition equal to the arithmetic mean of similarities between the sample and all members of the cluster. The equation is

$$S_{J(K)} = \frac{1}{t_J t_K} \left(\sum S_{JK} \right) ,$$

where $S_{J(K)}$ = Similarity between clusters *J* and *K*

t_J = Number of samples in cluster *J* (≥ 1)

t_K = Number of samples in cluster *K* (≥ 2).

Correspondence Analysis

This is a type of ordination, developed specifically for analysis of data on animal ecology, which is similar to principal components but uses instead of eigenvalues reciprocal averaging to determine axis values (Hill 1973). If two samples have similar profiles, i.e. the faunal composition on the trees investigated is similar, they are plotted closely together in the correspondence analysis. Squared distances between two sample points are approximately proportional to chi-square distances that test the homogeneity between both of them.

3. Results

A total of 192 trees (eight trees multiplied by four sampling sessions and six collecting units) were investigated, a total canopy volume of approximately 1657 m³ was exploited and 243,778 arthropods were collected from October 2001 to February 2003 (Fig. 10; Appendices 2−5). Since this work focuses mainly on beetles, the first part of this chapter will only mention very briefly the most dominant arthropod groups and the second part will deal with the beetles in detail.
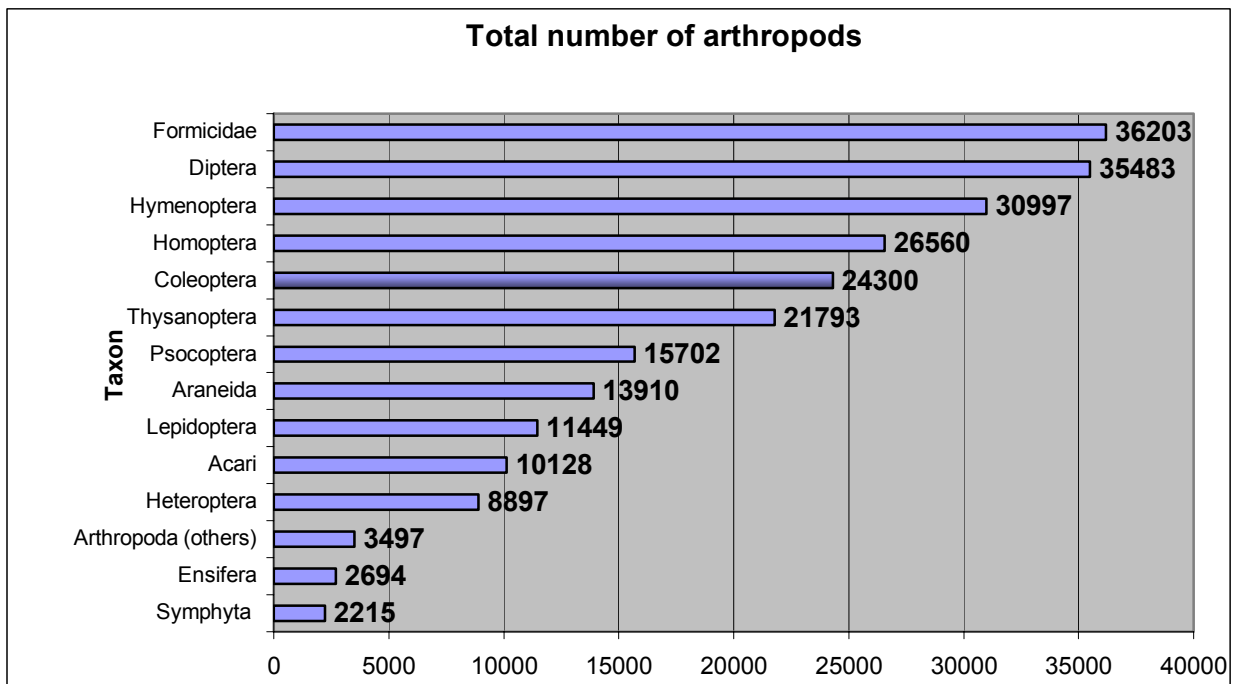
Fig. 9: Most abundant arthropod taxa (number of individuals) collected on 192 trees between X.2001 and I.2003.
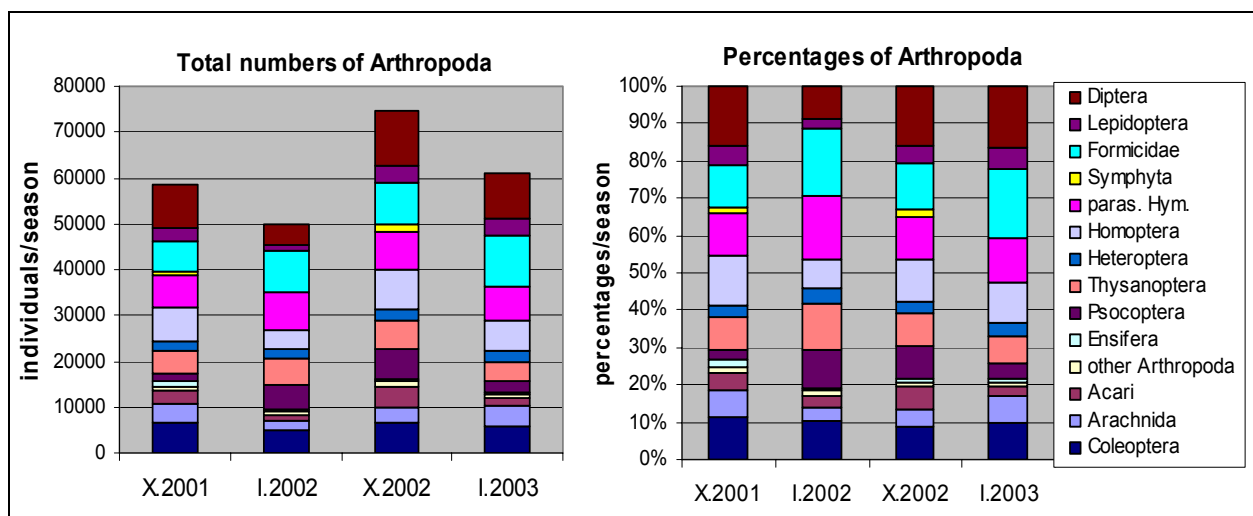
Fig. 10: Overview of the total numbers (left) and percentages (right) of arthropods per season, collected between X.2001 and I.2003.

3.1. Distribution patterns of arthropods

Formicidae was the most abundant group among all taxa investigated, taking all four sampling sessions into account (Fig. 9). A total of 36,203 ants were collected from October 2001 to February 2003. That was a proportion of 14.85 %. Diptera were also very abundant (35,483 individuals, 14.56 %), as well as parasitoid Hymenoptera (30,997 individuals, 12.72 %, excluding Symphyta) and Homoptera (26,560 individuals, 10.90 %). The Homoptera consists of Cicadoidea, Aphidoidea, Psylloidea, Coccoidea and Aleyrodoidea (in order of abundance, the latter two were very rare). A total of 24,300 beetles were found (23,187 adults and 1113 larvae), that was 9.97 % of the total number of arthropods. In Thysanoptera 21,793 individuals were collected (8.94 %). An overview of the total number and percentages of all collected arthropods for each season and sampling session respectively, is given in Fig. 10. For more details see also Appendices 2−5.
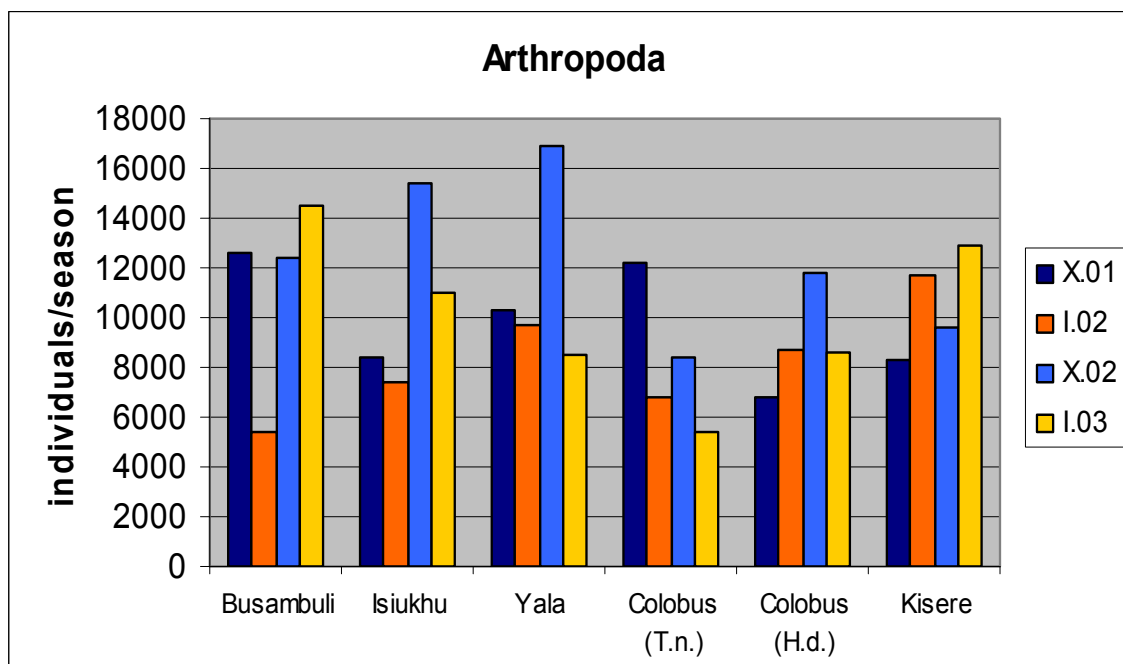
Fig. 11: Total numbers of arthropods collected per season at each study site; blue bars = wet seasons, orange bars = dry seasons. T.n. = *Teclea nobilis*, H.d. = *Heinsenia diervilleoides*.

3.1.1. Rainy season X. 2001

The 48 trees that were investigated during the first rainy season inhabited 58,540 arthropods with a mean of 1220 per tree (Fig. 12). The total individual numbers of arthropods do not differ significantly between the study sites. The most abundant

groups were Diptera (15.23 %), Homoptera (13.08 %), Formicidae (11.51 %) and parasitoid Hymenoptera (11.45 %). The representation of beetles and their larvae was 10.71 % and 0.81 % respectively.
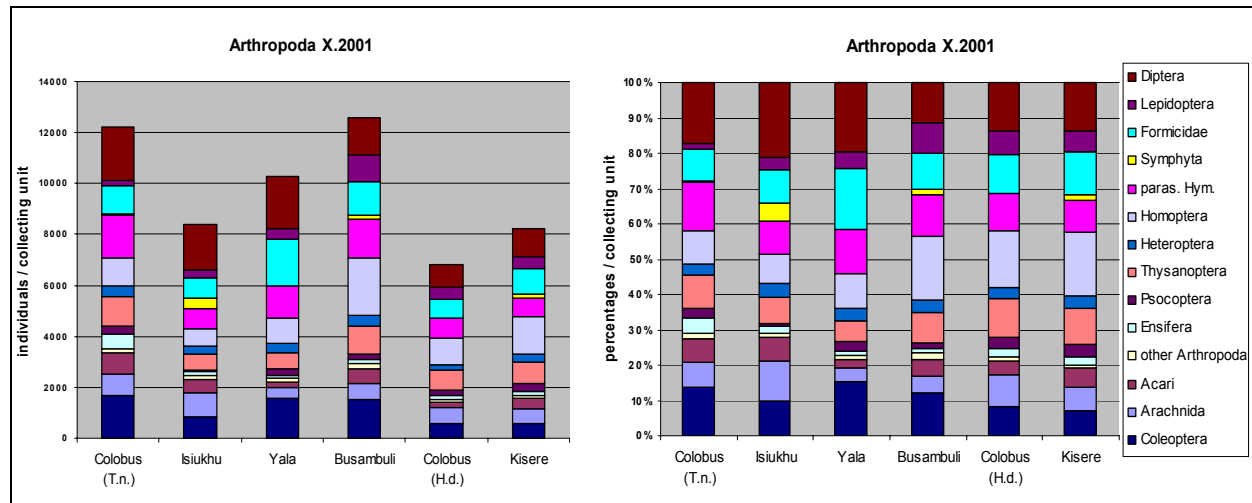
Fig. 12: Total numbers (left) and percentages (right) of arthropods collected in X.2001. T.n. = *Teclea nobilis*, H.d. = *Heinsenia diervilleoides*.

Colobus Trail (*Teclea nobilis*)

At the Colobus Trail 12,208 arthropods were collected on eight trees, with a mean number of 1526 per tree. The most dominant arthropod groups were Diptera, with a proportion of 16.33 %, parasitoid Hymenoptera (13.58 %) and Coleoptera (12.66 %). The latter were most abundant at this site and show significant differences compared with the sites at Isiukhu River, Colobus Trail (*Heinsenia*) and Kisere Forest (p < 0.001, Table 3). Ants have a proportion of 9.03 %. Remarkable was the large number of Ensifera, namely 533 individuals and 4.37 %, respectively. Thus, they were about three times more abundant than at all other sites, where the values ranged from 114 to 178 individuals (p < 0.001 for all sites). Spiders were significantly more abundant than in the Yala fragment (p < 0.01) and Psocoptera were more abundant than at the Isiukhu River (p < 0.05).

Isiukhu River

A total number of 8392 arthropods with a mean of 1049 per tree were recorded on the collecting unit along the Isiukhu River. Diptera were again the most dominant group with a proportion of 19.80 % and while Araneida were not very frequent in other assemblages during the first wet season (4.76−9.09 %), they were at the Isiukhu River with a proportion of 11.51 % and with significant differences compared with the abundances in the Yala fragment and Kisere Forest (p < 0.01, Table 3). Formicidae (9.38 %), parasitoid Hymenoptera (9.33 %) and beetles (8.91 %) were about the same

proportion. Larvae of Symphyta numbered 420 (5.00 %), whereas they were very rare in the other samples and values ranged from zero to 179 specimens. These differences were significant compared to the Kisere Forest, both collecting units at the Colobus Trail and the Yala forest fragment (p < 0.01).

Yala

A mean of 1284 arthropods per tree was collected in the Yala forest fragment, with a total number of 10,269 arthropods. Of these were 2002 flies and nematocerous dipterans and hence, Diptera were the most abundant group with a proportion of 19.50 %. Ants included 1798 individuals or a proportion of 17.51 %, more than at any other site (745−1308 individuals). Other abundant groups were beetles, with a proportion of 14.67 % and parasitoid Hymenoptera (12.51 %). Beetles were significantly more abundant than at the Colobus Trail (*Heinsenia*) and the Kisere Forest, p < 0.001, Table 3).

Busambuli River

Most of the arthropods during the first wet season, namely 12,579, were collected at the Busambuli River, with a mean of 1572 per tree. Remarkable was the high amount of Homoptera (2258 individuals), in particular aphids and cicadas. They were the most dominant group (17.95 %) and significantly more abundant than at the Isiukhu River, the Yala fragment and at the *Heinsenia*-collecting unit at the Colobus Trail (p < 0.01, Table 3). Parasitoid Hymenoptera (11.85 %) and Coleoptera (11.27 %) were more frequent than Diptera (10.93 %) and Formicidae (10.04 %). For beetle, values were significantly higher than at the Colobus Trail (*Heinsenia*) and Kisere Forest (p < 0.001). Caterpillars were represented by 1049 individuals or 8.34 %, and thus, they were much more abundant than at the other study sites (212−482 individuals) with significant differences compared to the sites at Isiukhu River and Colobus Trail (p < 0.05).

Colobus Trail (*Heinsenia diervilleoides*)

On eight trees of *Heinsenia* at Colobus Trail the least number of arthropods, namely 6834, were found, or a mean of only 854 per tree. The most abundant group were Homoptera with a proportion of 15.85 %, followed by Diptera (12.86 %) and parasitoid Hymenoptera (10.83 %). Least of all beetles were found on this collecting unit, namely 513 specimens (or 7.51 %), and even thrips (10.76 %), ants (10.74 %) and spiders (9.09 %) were more abundant.

Kisere

The sampling in the Kisere fragment revealed a total of 8258 arthropods with a mean of 1032 per tree. Most of them belonged to the Homoptera, with a proportion of 17.90 %,

Formicidae (12.23 %) and Diptera (12.18 %). Beetles were comparatively low in numbers; 537 could be found, or a proportion of 6.50 % and hence, it was the lowest one of all sites. Psocoptera were significantly more abundant than at the Isiukhu River ($p < 0.05$, Table 3).

Table 3: One-way ANOVA and Tukey-Kramer HSD post hoc test for major taxa of arthropods collected in X.2001. In case of multiple possibilities, sites are listed in order of decreasing means, i.e. increasing differences.

		Tukey-Kramer HSD post hoc test:		the site at			
		bus	**isi**	**yal**	**col**	**hein**	**kis**
X.2001	**ANOVA**	has significant higher values than the site(s) at					
Arachnida	< 0.01	-	yal,kis	-	yal	-	-
Acari	n.s.	-	-	-	-	-	-
Ensifera	< 0.001	-	-	-	bus,isi,yal,hein,kis	-	-
Psocoptera	< 0.05	-	-	-	isi	-	isi
Thysanoptera	n.s.	-	-	-	-	-	-
Heteroptera	n.s.	-	-	-	-	-	-
Homoptera	< 0.01	isi,yal,hein	-	-	-	-	-
Coleoptera	< 0.001	hein,kis	-	hein,kis	isi,hein,kis	-	-
Hymenoptera	< 0.05	-	-	-	-	-	-
Symphyta	< 0.01	-	kis,col,hein,yal	-	-	-	-
Formicidae	n.s.	-	-	-	-	-	-
Lepidoptera	< 0.05	isi,col	-	-	-	-	-
Diptera	n.s.	-	-	-	-	-	-
total	n.s.	-	-	-	-	-	-

3.1.2. Rainy season X. 2002

On all 48 trees a total of 74,492 arthropods were found during the second rainy season, with a mean of 1552 per tree. These were similar results to those of the first wet season (Fig. 13). The total individual numbers of arthropods do not differ significantly between the study sites (after post hoc test). Diptera was the most dominant group with a proportion of 15.58 %, followed by Formicidae (12.04 %), parasitoid Hymenoptera (11.51 %) and Homoptera (11.30 %). Coleoptera had a proportion of 8.32 % (6196 individuals); their larvae were represented by 294 individuals (0.39 %).

Colobus Trail (*Teclea nobilis*)

A total of 8424 arthropods, with an average of 1053 per tree, were collected at Colobus Trail. This was the lowest value of all samples and a high contrast to the first wet season (see above). Most were Diptera (22.97 %), Hymenoptera (15.56 %) and Thysanoptera (10.75 %). The numbers of ants and Symphyta (larvae) were conspicuously low, 6.55 % and 0.19 % respectively. Beetles were represented by 651 specimens (7.73 %).

Isiukhu River

A total of 15,423 arthropods were found on the trees along the Isiukhu River, an average of 1928 per tree. Acari was the most abundant group of all with a proportion of 15.01 %. A total of 2315 mites were recorded and by far the highest value from all trees investigated during this project (significantly higher values than for all other sites in this season, p < 0.001, Table 4). Diptera (14.58 %) and Hymenoptera (11.44 %) were also very abundant. Of beetles 912 were counted (5.91 %) and 830 larvae of Symphyta (5.38 %), which were much rarer at the other sites (p < 0.01, except the site at Busambuli River).

Yala

The most arthropods (16,902) during this season were recorded in the Yala fragment, i.e. 2113 on average per tree. Homoptera and in particular aphids were the most dominant group with a proportion of 20.02 % (significantly higher compared to all sites, p < 0.001, Table 4). Diptera (15.59 %) and parasitoid Hymenoptera (12.12 %) were also very abundant. And though the Coleoptera were only the fourth largest group in the Yala fragment with a proportion of 11.04 % (1866 individuals), they were almost three times more abundant than at Colobus Trail. At all other sites less beetles were found, where values ranged from 589 to 1552 (p < 0.001, except the site at Busambuli River).
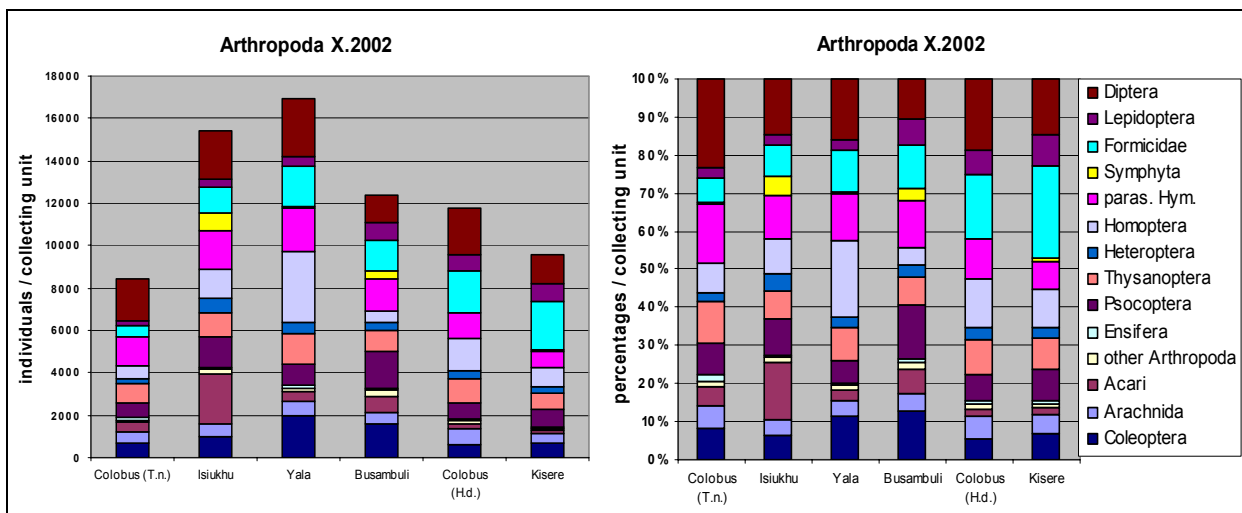
Fig. 13: Total numbers (left) and percentages (right) of arthropods collected in X.2002. T.n. = *Teclea nobilis*, H.d. = *Heinsenia diervilleoides*.

Busambuli River

Each tree averaged 1552 arthropods and a total number of 12,413 were collected. The most frequent insect group was Psocoptera with a proportion of 14.28 % (p < 0.05 compared to the site at Colobus Trail, Table 4) and Coleoptera with a proportion of

12.50 % (p < 0.001 for abundance compared to sites at Colobus Trail (*Heinsenia* and *Teclea*) and Kisere Forest). Also many Hymenoptera (12.21 %), Formicidae (10.82 %) and Diptera (10.59 %) were found. Remarkable was the high proportion of caterpillars (6.42 %), which were significantly more abundant than at Isiukhu River and Colobus Trail (p < 0.001).

Colobus Trail (*Heinsenia diervilleoides*)

In contrast to the first rainy season (see above), many more arthropods were collected during the second wet season on the *Heinsenia* collecting unit at Colobus Trail, namely 11,766 individuals in total and 1471 on average per tree. Diptera were the most abundant group with a proportion of 18.17 %, ants were 15.29 % and Homoptera were 12.91 %. There were again many larvae of Lepidoptera (6.39 %, p < 0.001 compared to the *Teclea* collecting unit at the same site, Table 4), even more than adult beetles (5.01 %, which was the smallest value of all sites).

Table 4: One-way ANOVA and Tukey-Kramer HSD post hoc test for major taxa of arthropods collected in X.2002. In case of multiple possibilities, sites are listed in order of decreasing means, i.e. increasing differences.

|		Tukey-Kramer HSD post hoc test:		the site at			
		bus	isi	yal	col	hein	kis
X.2002	**ANOVA**	has significant higher values than the site(s) at					
Arachnida	n.s.	-	-	-	-	-	-
Acari	< 0.001	-	bus,yal,col,hein,kis	-	-	-	-
Ensifera	n.s.	-	-	-	-	-	-
Psocoptera	< 0.05	col	-	-	-	-	-
Thysanoptera	n.s.	-	-	-	-	-	-
Heteroptera	n.s.	-	-	-	-	-	-
Homoptera	< 0.001	-	-	hein,isi,kis,col,bus	-	-	-
Coleoptera	< 0.001	col,kis,hein	-	isi,col,kis,hein	-	-	-
Hymenoptera	n.s.	-	-	-	-	-	-
Symphyta	< 0.01	-	yal,kis,hein,col	-	-	-	-
Formicidae	n.s.	-	-	-	-	-	-
Lepidoptera	< 0.001	isi,col	-	-	-	col	col
Diptera	n.s.	-	-	-	-	-	-
total	< 0.05	-	-	-	-	-	-

Kisere

Only a mean of 1195 specimens per tree and a total number of 9564 arthropods were collected in the Kisere forest. Ants were by far the most abundant group with a proportion of 22.99 %, followed by dipteran insects (13.99 %). Similar to *Heinsenia* at

Colobus Trail, on this collecting unit more caterpillars (8.31 %, p < 0.001 compared to Colobus Trail) than adult beetles (6.55 %) were found.

3.1.3. Dry season I. 2002

In the first dry season a total of 49,759 arthropods were found, with an average of 1037 per tree and thus least of all arthropods collected during all seasons (Fig. 10). The total individual numbers of arthropods were not significantly different between study sites. Most abundant were Hymenoptera with a proportion of 17.05 %, Formicidae (16.18 %), Thysanoptera (12.23 %) and Psocoptera (10.44 %). A total of 4947 adult beetles and 128 larvae were found, or 9.94 % and 0.26 %, respectively (see Fig. 14).
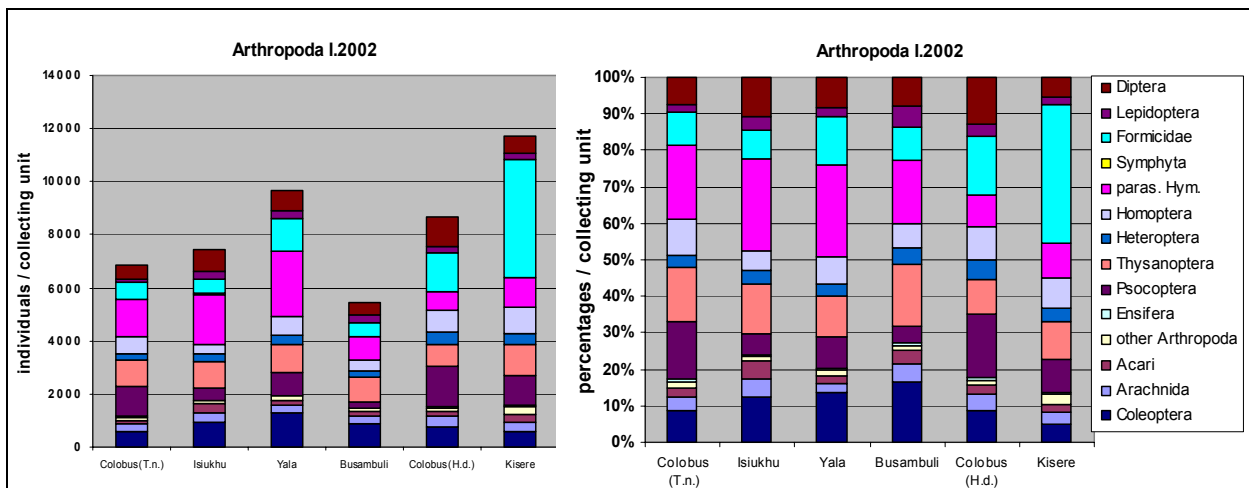
Fig. 14: Total numbers (left) and percentages (right) of arthropods collected in I.2002. T.n. = _Teclea nobilis_, H.d. = _Heinsenia diervilleoides_.

Colobus Trail (_Teclea nobilis_)

A total of 6843 arthropods with a mean number of 855 per tree were collected on the collecting unit of _Teclea_ at Colobus Trail. The most dominant groups were parasitoid Hymenoptera with a proportion of 20.34 %, Psocoptera (16.02 %, p < 0.01 compared to Busambuli River) and Thysanoptera (14.80 %). Only relatively few beetles were found (596 individuals, 8.71 %).

Isiukhu River

Parasitoid Hymenoptera were by far the most dominant group with a proportion of 25.25 % at Isiukhu River. Thysanoptera had a proportion of 13.85 % and beetles of 12.20 %. It is remarkable that during the dry season only eight Symphyta larvae were collected at this site and no more at any other site. The total number of arthropods was

7427 with a mean of 928 per tree. Mites were significantly more abundant than at Colobus Trail and the Yala fragment (p < 0.05, Table 5).

Yala

On each tree an average of 1209 arthropods were found, a total of 9676. Hymenoptera were again by far the most dominant group with a proportion of 25.28 % (p < 0.01 compared to Busambuli River and Colobus Trail (*Heinsenia*)), followed by ants (13.22 %) and beetles (13.17 %). Compared to the other sites, the most beetles were collected in the Yala forest fragment (1274 individuals at Yala, 581−848 at other sites, p < 0.05 compared to Colobus Trail and Kisere Forest).

Table 5: One-way ANOVA and Tukey-Kramer HSD post hoc test for major taxa of arthropods collected in I.2002. In case of multiple possibilities, sites are listed in order of decreasing means, i.e. increasing differences.

		Tukey-Kramer HSD post hoc test:		the site at			
		bus	isi	yal	col	hein	kis
I.2002	**ANOVA**	has significant higher values than the site(s) at					
Arachnida	< 0.05	-	-	-	-	-	-
Acari	< 0.05	-	yal,col	-	-	-	-
Ensifera	n.s.	-	-	-	-	-	-
Psocoptera	< 0.01	-	-	-	bus	isi,bus	-
Thysanoptera	n.s.	-	-	-	-	-	-
Heteroptera	< 0.01	-	-	-	-	bus,col	-
Homoptera	< 0.05	-	-	-	-	-	isi,bus
Coleoptera	< 0.05	-	-	col,kis	-	-	-
Hymenoptera	< 0.01	-	-	bus,hein	-	-	-
Symphyta	< 0.05	-	-	-	-	-	-
Formicidae	n.s.	-	-	-	-	-	-
Lepidoptera	< 0.05	col	-	-	-	-	-
Diptera	n.s.	-	-	-	-	-	-
total	n.s.	-	-	-	-	-	-

Busambuli River

Least of all arthropods were collected at this site, namely 5422, with a mean of 678 per tree. Remarkable were also the few Psocoptera (4.37 %). Most insects belonged to Hymenoptera with a proportion of 17.10 %, Thysanoptera (17.00 %) and Coleoptera (15.64 %). Nevertheless, caterpillars were significantly more abundant than at Colobus Trail (302 individuals at Busambuli River and 115 at Colobus Trail, p < 0.05, Table 5).

Colobus Trail (*Heinsenia diervilleoides*)

A total of 8688 arthropods were found on the collecting unit of *Heinsenia*, with a mean of 1086 per tree. Most abundant were Psocoptera with a proportion of 17.33 %

(p < 0.01 compared to sites at Busambuli and Isiukhu River, Table 5), Formicidae (16.28 %) and Diptera (11.36 %). Coleoptera had a proportion of 8.54 %. Heteroptera were significantly more abundant than at Busambuli River and Colobus Trail (p < 0.01).

Kisere

Most of all arthropods during the first dry season were recorded from Kisere. It totaled 11,703 individuals and a mean of 1463 per tree. Over one-third of them were ants and their carried larvae with proportions of 31.21 % and 6.84 %, respectively, but most of them were collected on a single tree (3280 of 4452 individuals). Many thrips were collected, namely 1215 individuals with a proportion of 10.38 %. Only few beetles were found and the lowest number (581 individuals) and proportion (4.96 %) of all sites studied. Homoptera were significantly more abundant than at Isiukhu and Busambuli River (p < 0.05, Table 5).

3.1.4. Dry season I. 2003

A total of 60,987 arthropods were found during the second dry season, with a mean of 1271 per tree. Thus, this assemblage revealed many more individuals than the assemblage of the first dry season (n = 49,759) and even more than the one from the first wet season (n = 58,540, see Fig. 15). The total individual numbers of arthropods were significantly higher at Busambuli River and in Kisere Forest than at Colobus Trail (p < 0.01). A total of 10,295 ants were collected and thus it was the most dominant group with a proportion of 16.88 %. Diptera (16.24 %) and Hymenoptera (11.87 %) were also abundant groups and Coleoptera had a proportion of 9.39 %, their larvae of 0.36 %.

Colobus Trail (*Teclea nobilis*)

Least of all arthropods in this season were found at the Colobus Trail; only 5405 individuals, i.e. 676 on average per tree. The most dominant groups were Diptera with a proportion of 26.22 %, Hymenoptera (16.87 %) and Coleoptera (10.77 %). Remarkably few ants were collected (7.40 %), and also butterfly larvae (2.04 %) and Psocoptera (1.07 %) were very rare. Although the collecting unit of *Teclea* yielded the least of all arthropods, most of the Ensifera were found here. They were significantly more abundant than at Isiukhu River and in the Kisere Forest (p < 0.05, Table 6).

Isiukhu River

A total of 11,045 arthropods and on average 1381 per tree were collected along the Isiukhu River. Diptera were again the most abundant group with a proportion of

21.44 %, followed by Hymenoptera (13.32 %) and Formicidae (12.59 %). Beetles were represented by 827 specimens, with a portion of 7.94 %. Some taxa showed significant differences in abundances, namely spiders (p < 0.05, compared to Colobus Trail, Table 6), mites (p < 0.001, compared to Colobus Trail (*Heinsenia* and *Teclea* collecting units) and the Yala forest fragment), psocids (p < 0.01, compared to Colobus Trail (*Heinsenia* and *Teclea* collecting units) and caterpillars (p < 0.001, compared to Colobus Trail).
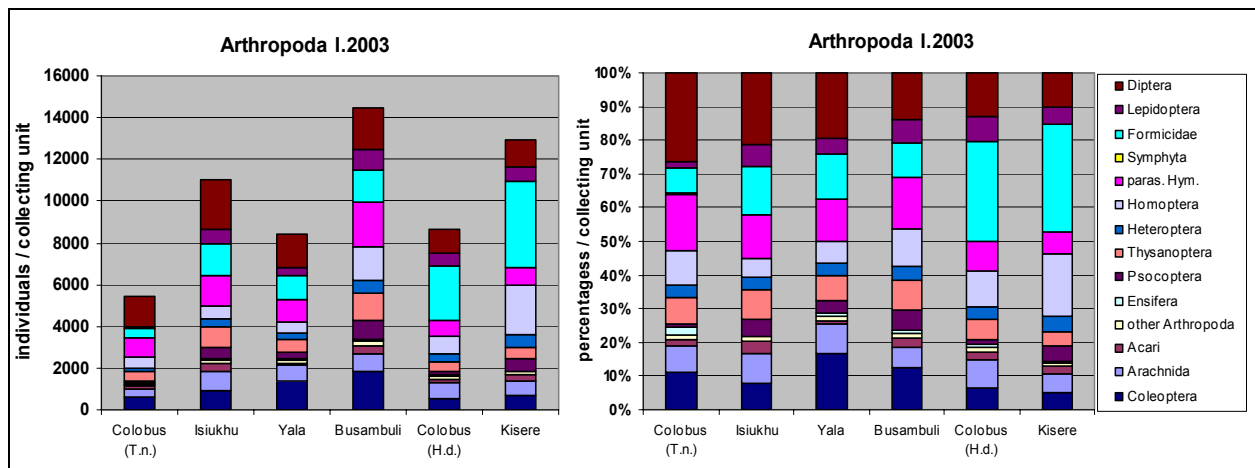
Fig. 15: Total numbers (left) and percentages (right) of arthropods collected in I.2003. T.n. = *Teclea nobilis*, H.d. = *Heinsenia diervilleoides*.

Yala

On each tree, a mean 1057 arthropods were found, for a total number of 8456. The most abundant groups were Diptera with a proportion of 19.50 %, Coleoptera (16.38 %), Formicidae (13.22 %) and Hymenoptera (12.46 %). Beetles were significantly more abundant than in the Kisere Forest and at Colobus Trail (*Heinsenia* and *Teclea* collecting units) (p < 0.001, Table 6).

Busambuli River

The highest amount of arthropods per collecting unit was collected at the Busambuli Trail, namely 14,496 individuals in total and 1812 on average per tree. Most of them belonged to the Hymenoptera (15.25 %), Diptera (13.90 %) and Coleoptera (12.15 %), the latter was the most numerous at this site (1761 individuals; 536−1385 at other sites). Also remarkable was the high number of caterpillars (991 individuals; 110−679 at other sites). Due to the enormous number of arthropods collected, almost every taxon had significantly higher values than at the other sites and even the total number of arthropods was significantly different (p < 0.01 compared to the site at Colobus Trail), for details see Table 6.

Colobus Trail (*Heinsenia diervilleoides*)

A total of 8636 arthropods and a mean number of 1079 per tree were found. Formicidae had a very high proportion of this number, namely 25.95 % and were the most dominant group. Diptera (12.98 %) and Homoptera (10.38 %) were also abundant groups. Only 536 beetles and 6.21 % respectively, were found and this was the lowest number in all sites. Caterpillars were significantly more abundant than on the *Teclea* collecting unit at this site (p < 0.001, Table 6).

Table 6: One-way ANOVA and Tukey-Kramer HSD post hoc test for major taxa of arthropods collected in I.2003. In case of multiple possibilities, sites are listed in order of decreasing means, i.e. increasing differences.

		Tukey-Kramer HSD post hoc test:	the site at				
		bus	**isi**	**yal**	**col**	**hein**	**kis**
I.2003	**ANOVA**	has significant higher values than the site(s) at					
Arachnida	< 0.05	col	col	-	-	-	-
Acari	< 0.001	col,yal	hein,col,yal	-	-	-	-
Ensifera	< 0.05	-	-	-	kis,isi	-	-
Psocoptera	< 0.01	yal,hein,col	hein,col	-	-	-	hein,col
Thysanoptera	< 0.001	yal,kis,hein,col	-	-	-	-	-
Heteroptera	< 0.01	col	-	-	-	-	col
Homoptera	n.s.	-	-	-	-	-	-
Coleoptera	< 0.001	isi,kis,col,hein	-	kis,col,hein	-	-	-
Hymenoptera	< 0.01	yal,col,kis,hein	-	-	-	-	-
Symphyta	n.s.	-	-	-	-	-	-
Formicidae	< 0.05	-	-	-	-	-	col
Lepidoptera	< 0.001	kis,hein,yal,col	col	-	-	col	col
Diptera	n.s.	-	-	-	-	-	-
total	< 0.01	col	-	-	-	-	col

Kisere

On each tree a mean number of 1618 and a total number of 12,949 arthropods were collected. As in I.2002, the ants were enormously abundant with a proportion of 28.41 % adults and 3.58 % larvae and pupae respectively, but again most of them were collected on a single tree, which was the same tree as in the first dry season. Homoptera revealed a proportion of 18.52 %, Diptera of 10.32 % and Coleoptera of only 4.91 % and 636 individuals, respectively. The total number of arthropods was significantly higher than at Colobus Trail, in particular caterpillars, ants, bugs and psocids were more abundant, the latter at both collecting units at Colobus Trail (see Table 6).

3.2. Distribution patterns and diversity of beetles

During the field work from October 2001 to January 2003 a total of 23,187 adult beetles, which could be allocated to 1023 species, and 1113 beetle larvae were collected. The overall most abundant group was Corylophidae (Fig. 16). A total of 4081 individuals of these mycetophagous beetles were collected, or 17.60 % of all adult beetles.
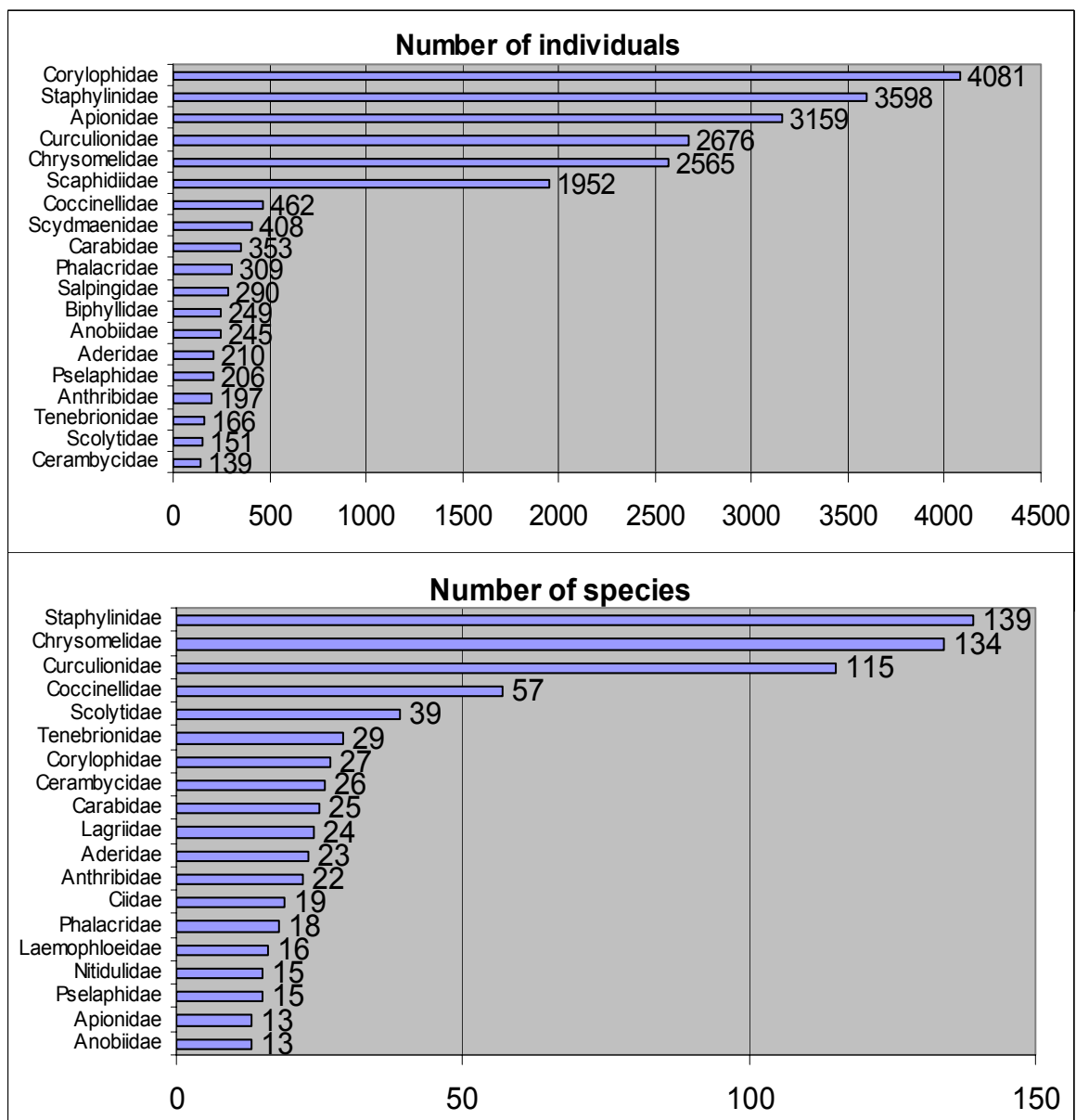
Fig. 16: Numbers of individuals (top) and species (bottom) of beetles among the most common taxa collected from X.2001 to II.2003.

Staphylinidae are represented by 3598 individuals (15.52 %) and Apionidae by 3159 individuals (13.62 %). Chrysomelidae are represented by 134 species and 2565 specimens (11.06 %). Staphylinidae, as the most species rich group, are represented by 139 species. The Corylophidae are assigned to 27 species and the Apionidae to 13

species. Curculionidae are very abundant and species rich, with 2676 individuals (11.54 %) allocated to 115 species. Another individual rich group is Scaphidiidae, with 1952 individuals (8.42 %) allocated to eight species. A detailed list of individuals and morpho-types of all beetle taxa is given in Appendix 6.

3.2.1. Diversity at different forest sites

There were significant differences in species diversity ($p < 0.001$) and individual numbers ($p < 0.01$) between the study sites. The highest individual numbers of beetles were collected at Busambuli River and in the Yala forest section (Fig. 17). A total of 5701 individuals and 880 species were found at the Busambuli River Trail during the field work. While most species were found at this site, the most individuals were collected in the Yala forest fragment (6011). They were allocated to a similar number of species as at the Busambuli River. Along the Isiukhu River the samples revealed a much lower number of individuals and species, with 3364 individuals and 766 species. On *Teclea nobilis* at the Colobus Trail a total of 3323 individuals allocated to 721 species were collected. The fewest beetles (2383 individuals and 558 species) were collected on *Heinsenia diervilleoides* at Colobus Trail. The assemblages in Kisere Forest revealed the lowest number of beetle species.
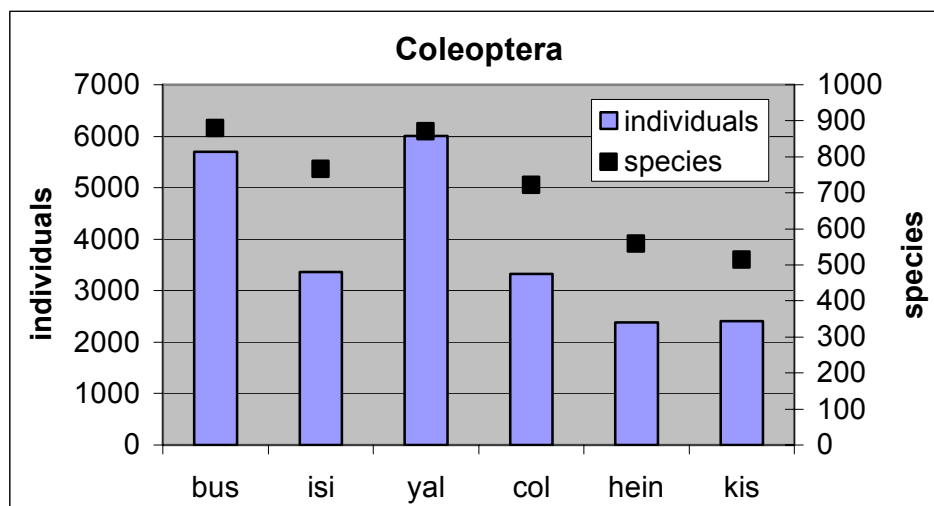
Fig. 17: Total number of individuals and species at each study site, collected from X.2001 to II.2003.

A comparison of the two sites in the Yala fragment and at Busambuli River (with the highest numbers of individuals and species) with the two sites at Colobus Trail (*Heinsenia*) and Kisere Forest (with the lowest number of individuals and species) shows, that the differences between these sites are highly significant for abundance

(p < 0.001) as well as for species numbers (p < 0.01). The species richness and abundance at Colobus Trail (*Teclea*) and along the Isiukhu River do not show any significant differences to the other study sites.

3.2.2. Diversity at different seasons

There were significant differences in individual numbers (p < 0.05) between wet and dry seasons, with higher numbers in the dry season; differences in species numbers were not significant. In the first wet season in October 2001, a total of 6335 individuals allocated to 556 species were collected (Fig. 18).
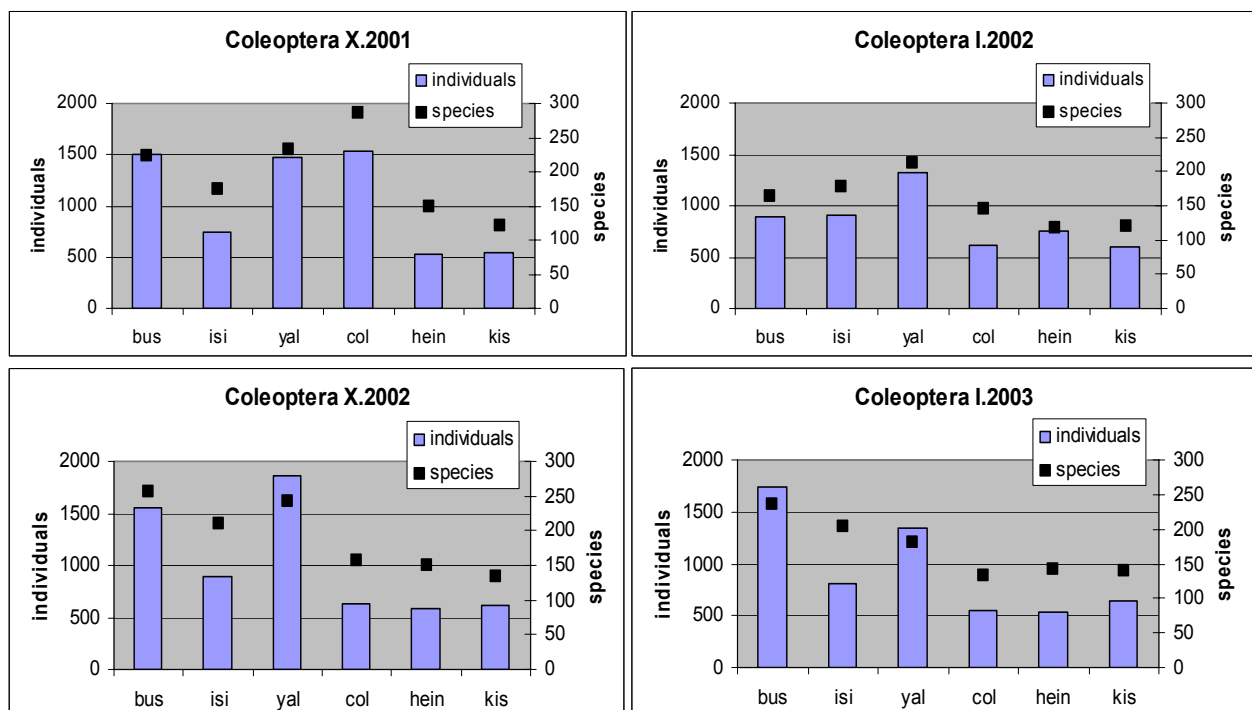
Fig. 18: Total number of individuals and species of beetles per site for each sampling period from X.2001 to II.2003. Wet seasons are on the left, dry seasons on the right.

The site with the highest beetle abundance and species richness was Colobus Trail, where 1532 individuals in 287 species were found (p < 0.001 for numbers of individuals compared with *Heinsenia* at Colobus Trail, Isiukhu River and Kisere). Similar numbers of individuals, but less numbers of species were found at Busambuli River and at the Yala fragment. These differences are highly significant for numbers of individuals compared with *Heinsenia* at Colobus Trail and Kisere (p < 0.001). Comparatively few beetles were collected along the Isiukhu River (745 individuals, 174 species), on the collecting unit of *Heinsenia* at Colobus Trail (521 individuals, 149 species) and in the

Kisere fragment (548 individuals, 122 species), where the lowest number of species was found.

In the second wet season, a total of 6129 individuals allocated to 524 species were collected, similar values to those of the wet season in X.2001. But contrary to the first wet season, in this season much fewer beetles were found on *Teclea* at Colobus Trail. Many more beetles and the highest number of species of all sites, namely 256 species, were found at Busambuli River Trail ($p < 0.001$ for numbers of individuals compared with both collecting units at Colobus Trail and Kisere Forest). The beetle fauna at the Yala forest site was most abundant ($p < 0.001$ for numbers of individuals compared with all sites, except of Busambuli River). Along the Isiukhu River, the samples yielded a total number of 895 beetles allocated to 210 species. The collecting unit of *Heinsenia* and samples in Kisere Forest were clearly lower in individuals and species numbers ($p < 0.001$ compared with the sites at Busambuli River and in the Yala fragment).

In the first dry season, a total of 5092 individuals allocated to 451 species were collected. The Yala fragment represented the most abundant and species rich beetle fauna of this season ($p < 0.05$ for numbers of individuals compared with Colobus Trail and Kisere). Much fewer beetles than in the wet seasons were found at Busambuli River and species and individual numbers were similar to those at Isiukhu River. Again very few beetles have been collected at both collecting units at Colobus Trail and in the Kisere Forest.

A total of 5631 individuals allocated to 502 species were collected during the second dry season in January 2003. Most of them were found at Busambuli River (1736 individuals, 237 species; $p < 0.001$ for numbers of individuals compared with all sites, except of the Yala fragment). Remarkable is the high number of species at Isiukhu River, although relatively few individuals were collected at that site. Many more beetles were found at the Yala fragment ($p < 0.001$ for abundances compared with both collecting units at Colobus Trail and Kisere), but less species than at Isiukhu River. The lowest number of species of all sites was found on *Teclea* at Colobus Trail. Few individuals and species were also collected on the collecting unit of *Heinsenia* and in the Kisere fragment.

3.2.3. Feeding guilds

To study the species richness and composition of the beetle fauna for each study site, selected dominant groups were chosen, on the basis of abundance or species richness. These groups were predacious beetles (Carabidae, Staphylinidae, including

Pselaphinae), mycetophagous beetles (Mycetophagidae, Biphyllidae, Corylophidae, Cryptophagidae, Latridiidae) and the two phytophagous groups of leaf beetles (Chrysomelidae) and weevils (Curculionidae, Apionidae).
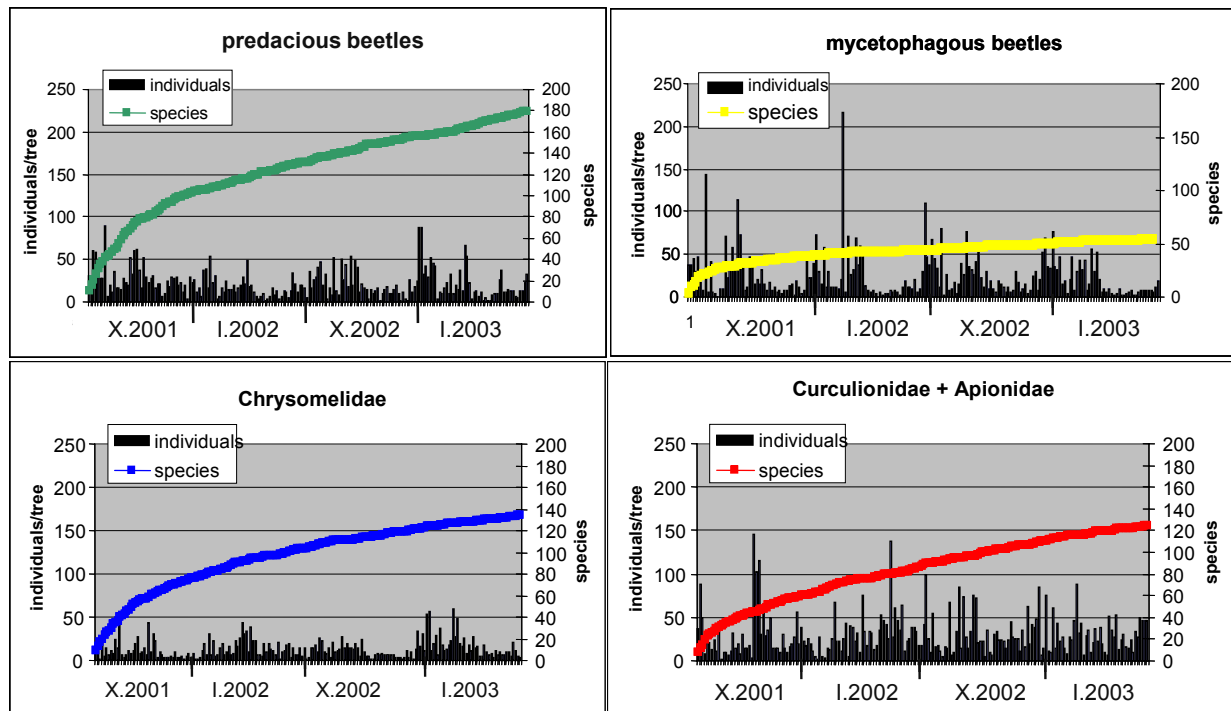
Fig. 19: Overview of the feeding guilds collected on 192 trees from X.2001 to I.2003. Each graph shows the collected individuals per tree and a species accumulation curve resulting in the total number of species per group.

3.2.3.1. Predacious beetles

By pooling the numbers of individuals and species of Carabidae (353 individuals, 25 species), Staphylinidae (3598/139) and Pselaphinae (206/15), the assemblages collected from October 2001 to February 2003 revealed a total of 4157 carnivorous beetles allocated to 179 species. The species accumulation curve for this group does not reach a plateau, which means that with every sampled tree a proportion of "new" species was found (Fig. 19). Pooled species numbers were highest for Yala and lowest for Kisere, but even between these study sites differences were not significant. The analysis of wet and dry seasons showed that mean species and individual numbers of wet seasons were higher than those of dry seasons. These differences were highly significant ($p < 0.001$ for species, $p < 0.05$ for individuals).

In the first wet season the numbers of individuals per study site ranged from 148 to 354, allocated to 38−59 species (Table 7). The most species were found on *Teclea* at Colobus Trail and in the Yala fragment, least of all in the Kisere Forest. Most abundant

were the predacious beetles at the Yala fragment and at Busambuli River. The rarefaction curve revealed expected species numbers between 27 and 38 for the smallest common random sample of 91 individuals (Fig. 20). Contrary to the species numbers observed, now least of all species were expected for the Busambuli River Trail and the fragments in Yala and Kisere. This was also recognisable on the more even courses of the rarefaction curves, whereas the curves for Colobus Trail and Isiukhu River were steeper, and most of the species were expected at these sites. Generally, dominance of single species was quite low; the proportion of singletons was relatively high, ranging from 35 to 48 % per site. This was also reflected in the very low diversity indices and the large evenness indices, respectively, with exception of the indices for Busambuli River, which were somewhat out of the range.

The results for the second wet season were very similar to those of the first wet season. The numbers of individuals ranged from 89 to 254, allocated to 25−50 species (Table 7). Remarkable was the low number of species observed at Colobus Trail, which was the highest number in October 2001. Fewer species were found only in the Kisere fragment, whereas most of all species were found at Isiukhu River and in the Yala forest section. Most abundant were again the samples from the Yala fragment and Busambuli River. However, the comparison of the rarefaction curves showed that the sites at Isiukhu River, Colobus Trail (both collecting units) and in the Yala fragment were supposed to be more diverse than at the other sites (Fig. 20). Dominance of single species was generally low, but somewhat higher at Busambuli River Trail. The comparison of species numbers for the random sample (n_{ind} = 100) between both wet seasons showed that most of the carnivorous species were found at Colobus Trail and along the Isiukhu River and least of all in Kisere Forest and at Busambuli River; these differences were significant ($p < 0.01$, n = 10). Remarkable in this season was the high ICE value for *Heinsenia* at Colobus Trail. Due to the high proportion of singletons at this site (53 %, others 35−42 %) a species number of 134 was estimated, which was almost four times as many as the observed number (Table 7).

Generally less species were collected during the dry season in January 2002. The assemblages yielded 49 to 222 individuals, which could be allocated to 23 to 33 species (Table 7). Most abundant were the predacious beetles at Busambuli River and in the Yala fragment, most species were found in Yala and along the Isiukhu River. The rarefaction curve revealed expected species numbers between 13 and 24 for the smallest common random sample of 51 individuals (Fig. 20). Most of the rarefied species numbers were found at Colobus Trail, which had the steepest of all curves. Least of all species were estimated for Busambuli River, the Yala fragment and Kisere Forest. This was also shown by the low evenness. The proportion of singletons was similar to those of the wet seasons, ranging from 39 to 52 %.

The results for the second dry season were very similar to those of the first. The sites with the highest individual numbers were the Yala fragment and Busambuli River, the latter revealed also the highest number of all species, but dominance of single species was quite high at both sites (Table 7). In Kisere Forest the lowest number of species was found. The rarefaction curve revealed expected species numbers between 13 and 24 for the random sample of 51 individuals (Fig. 20) and again most of the species were

Table 7: Species diversity of predacious beetles. S_{Obs} = Species observed, N = number of individuals, Singletons = species represented in the sample with only one specimen, ACE, ICE, Chao 1 = richness estimators, D = Simpson's Diversity Index and J' = Shannon's evenness index.

X.2001	bus	isi	yal	col	hein	kis
S_{obs}	49	42	56	59	43	38
N	354	148	299	222	165	148
Singletons	17	15	27	26	17	17
ACE	65	59	96	95	60	59
ICE	78	72	108	111	67	57
Chao 1	64	51	100	84	58	66
Simpson (D)	0.14	0.04	0.10	0.04	0.05	0.06
Evenness (J')	0.70	0.90	0.80	0.87	0.87	0.86
I.2002	bus	isi	yal	col	hein	kis
S_{obs}	26	29	33	24	25	23
N	222	113	185	49	75	140
Singletons	12	12	16	12	13	9
ACE	44	46	58	38	49	31
ICE	50	57	57	52	60	34
Chao 1	43	36	53	34	38	30
Simpson (D)	0.20	0.09	0.22	0.04	0.08	0.25
Evenness (J')	0.65	0.83	0.67	0.93	0.86	0.67
X.2002	bus	isi	yal	col	hein	kis
S_{obs}	42	50	49	33	36	25
N	247	179	254	89	104	99
Singletons	18	21	17	16	19	10
ACE	62	70	64	52	65	40
ICE	78	97	80	64	134	45
Chao 1	59	76	64	57	65	32
Simpson (D)	0.19	0.04	0.08	0.04	0.06	0.09
Evenness (J')	0.69	0.89	0.81	0.92	0.88	0.84
I.2003	bus	isi	yal	col	hein	kis
S_{obs}	36	31	27	24	30	22
N	417	116	232	52	129	119
Singletons	17	16	11	19	13	11
ACE	62	57	43	131	50	39
ICE	82	65	44	152	63	37
Chao 1	64	55	35	112	41	36
Simpson (D)	0.31	0.09	0.32	0.11	0.16	0.17
Evenness (J')	0.53	0.82	0.59	0.83	0.74	0.72
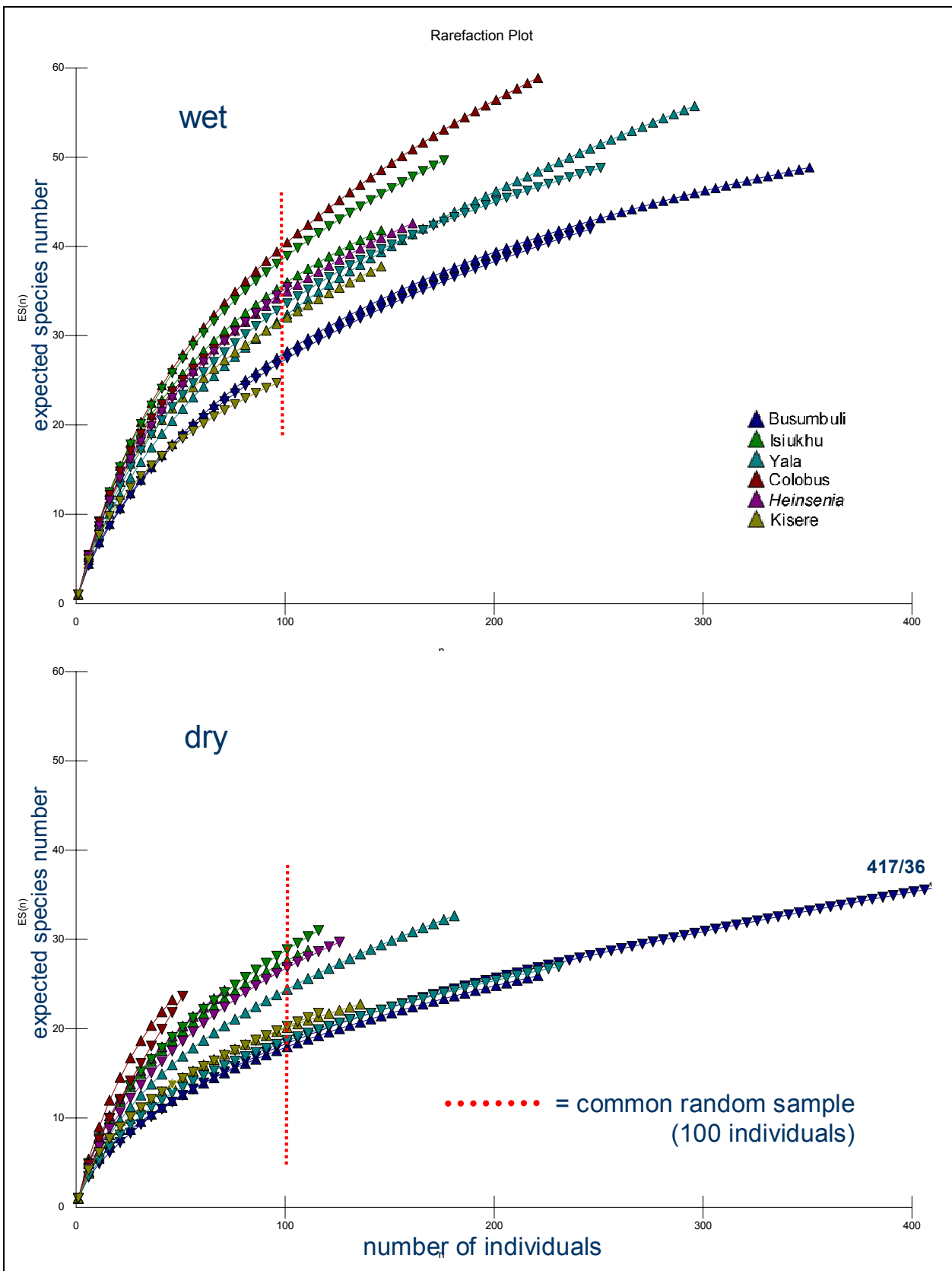
Fig. 20: Rarefaction plot of both wet seasons (top) and both dry seasons (bottom) for predacious beetles; ▲= X.2001,I.2002; ▼=X.2002,I.2003.

Fig. 21: Cluster analysis for predacious beetles. Each collecting unit is represented by four samples (1 = X.2001 (wet), 2 = I.2002 (dry), 3 = X.2002 (wet), 4 = I.2003 (dry)). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.

Fig. 22: Correspondence analysis for predacious beetles. Each collecting unit is represented by four samples (two wet and two dry seasons). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.

expected for Colobus Trail, although only 52 individuals were collected. Remarkable was also the very high proportion of singletons (73 %) at this site (others varied between 41 and 51 %), which led to an estimation of enormous species numbers of the richness estimators (up to 152 species, which is more than six times of the species observed). Least of all species were expected for the sites at Busambuli River, the Yala fragment and Kisere Forest. The comparison of species numbers for the common random sample (n_{ind} = 100) between both dry seasons showed that most of the carnivorous species were found along Isiukhu River and on *Heinsenia* at Colobus Trail. These differences were significant ($p < 0.05$, n = 9), compared with the species numbers in Kisere Forest, the Yala fragment and at Busambuli River.

The results of the Cluster Analysis showed two distinct clusters for dry and wet seasons (Fig. 21). Similarities between the same sites were generally low, nevertheless, within the "dry season cluster" the collecting units of Colobus Trail (*Heinsenia* and *Teclea*) and of Kisere Forest built a cluster each and within the "wet season cluster" the collecting units of the Yala fragment and of the Busambuli site built a cluster each. This was an indication that the beetle fauna was also influenced by the different forest types at the study sites. Also the Correspondence Analysis underlined the strong seasonal influence on the predacious beetles (Fig. 22). Since the collecting units of *Heinsenia* and *Teclea* were neither clustered nor grouped, a pattern within or between both tree species was not recognisable.

Faunal overlap within seasons

Faunal overlap between and within the study sites, seasons and both tree species was calculated with the Morisita-Horn Index. Within the wet season of X.2001 faunal overlap between sites varied between 10 and 69 % (Fig. 23). Highest overlap was within the trees of the collecting unit at Busambuli River (69 %), within the Yala fragment (47 %) and between Busambuli and Yala (54 %). Overlap between both tree species was generally low (10 to 24 %), within the tree species of *Heinsenia* (hein1-hein1 and kis1-kis1) slightly higher, namely 29 % and 26 %. The same pattern occured during the second wet season of X.2002. Values of faunal overlap ranged from 12 to 44 %, where highest values were within the Busambuli River (44 %), within the Yala fragment (35 %) and between Busambuli and Yala (38 %). During the dry season of I.2002 overlap varied between 15 and 57 %. It was high within Busambuli River (57 %), the Yala fragment (55 %), Kisere Forest (48 %) and between Yala-Kisere (50 %) and Yala-Busambuli (46 %). Highest values in I.2003 reached up to 73 %, found within the collecting unit of the Busambuli River Trail and between Yala-Busambuli (60 %). Between other sites, faunal overlap ranged from 10 to 48 %.

Faunal overlap between seasons

Most of the values were lower than 20 % and only values within Busambuli River (41−54 %), within the Yala fragment (30−52 %) and between Yala-Busambuli (28−61 %) were higher. Generally, the values showed a higher overlap between both dry seasons than between both wet seasons. Overlap between and within both tree species was low. Exceptions were shown in the comparisons of season 2 with 3 (I.2002 and X.2002) and season 2 with 4 (I.2002 and I.2003), where faunal overlap between Kisere-Yala was also high (44 and 57 %).

Pred	bs1	isi1	yal1	col1	hei1	kis1	bs2	isi2	yal2	col2	hei2	kis2	bs3	isi3	yal3	col3	hei3	kis3	bs4	isi4	yal4	col4	hei4	kis4
bus1	**0.69**																							
isi1	0.17	**0.25**																						
yal1	0.54	0.12	**0.47**																					
col1	0.13	0.16	0.11	**0.19**																				
hein1	0.18	0.23	0.14	0.24	**0.29**																			
kis1	0.11	0.21	0.10	0.21	0.26	**0.23**																		
bus2	**0.43**	0.14	0.28	0.08	0.13	0.12	**0.57**																	
isi2	0.30	**0.17**	0.19	0.09	0.14	0.09	0.30	**0.23**																
yal2	0.50	0.17	**0.34**	0.10	0.13	0.08	0.46	0.33	**0.55**															
col2	0.21	0.06	0.14	**0.09**	0.07	0.06	0.24	0.15	0.21	**0.16**														
hein2	0.29	0.10	0.17	0.09	**0.16**	0.12	0.38	0.21	0.30	0.23	**0.34**													
kis2	0.43	0.13	0.28	0.09	0.11	**0.09**	0.38	0.27	0.50	0.19	0.25	**0.48**												
bus3	**0.54**	0.15	0.36	0.11	0.16	0.10	**0.41**	0.27	0.49	0.19	0.28	0.44	**0.44**											
isi3	0.26	**0.21**	0.22	0.12	0.20	0.20	0.19	**0.17**	0.18	0.09	0.17	0.15	0.20	**0.17**										
yal3	0.43	0.16	**0.34**	0.13	0.17	0.11	0.31	0.24	**0.42**	0.15	0.25	0.33	0.38	0.20	**0.35**									
col3	0.21	0.11	0.17	**0.13**	0.13	0.09	0.11	0.10	0.13	**0.14**	0.13	0.10	0.17	0.12	0.16	**0.15**								
hein3	0.20	0.11	0.16	0.15	**0.18**	0.12	0.11	0.12	0.14	0.12	**0.18**	0.09	0.17	0.15	0.18	0.20	**0.24**							
kis3	0.29	0.17	0.20	0.10	0.14	**0.13**	0.22	0.17	0.25	0.11	0.19	**0.22**	0.27	0.18	0.22	0.17	0.19	**0.19**						
bus4	**0.53**	0.14	0.32	0.09	0.12	0.07	**0.53**	0.35	0.61	0.22	0.31	0.57	**0.54**	0.16	0.39	0.11	0.11	0.25	**0.73**					
isi4	0.45	**0.19**	0.30	0.13	0.15	0.12	0.38	**0.31**	0.46	0.23	0.28	0.39	0.41	**0.21**	0.34	0.17	0.18	0.25	0.47	**0.39**				
yal4	0.45	0.16	**0.30**	0.10	0.11	0.08	0.43	0.29	**0.52**	0.18	0.25	0.47	0.45	0.16	**0.34**	0.12	0.11	0.23	0.60	0.40	**0.48**			
col4	0.06	0.14	0.04	**0.05**	0.07	0.06	0.15	0.11	0.08	**0.09**	0.10	0.05	0.06	0.08	0.06	**0.10**	0.12	0.14	0.10	0.13	0.11	**0.14**		
hein4	0.22	0.18	0.16	0.10	**0.15**	0.10	0.35	0.24	0.26	0.16	**0.24**	0.19	0.21	0.14	0.21	0.14	**0.20**	0.21	0.30	0.26	0.27	0.26	**0.37**	
kis4	0.34	0.24	0.24	0.10	0.13	**0.12**	0.33	0.28	0.44	0.17	0.23	**0.37**	0.35	0.18	0.30	0.16	0.19	**0.30**	0.42	0.40	0.40	0.21	0.33	**0.48**

Legend: <25, 25<40, 40<55, 55<70, ≥70

Fig. 23: Faunal overlap of predacious beetles (4157 ind./179 ssp.) within and among study sites and seasons, calculated with the Morisita-Horn Index. Numbers added to the abbreviations of the study sites represent the seasons: 1 = X.2001, 2 = I.2002; 3 = X.2002; 4 = I.2003. Bus, isi, yal and col = *Teclea nobilis*, hein and kis = *Heinsenia diervilleoides*.

3.2.3.2. Mycetophagous beetles

Numbers of individuals and species of Mycetophagidae (83 individuals, 7 species), Biphyllidae (249/8), Corylophidae (4081/27), Cryptophagidae (63/3) and Latridiidae (102/9) from samples of October 2001 to January 2003 revealed a total of 4578 mycetophagous beetles allocated to 54 species. The species accumulation curve (Fig. 19) reached nearly a plateau after the first sampling period and afterwards new species were only found rarely. The mean species numbers were high for Busambuli River, Isiukhu River and the Yala fragment and low for *Heinsenia* at Colobus Trail and the

Kisere fragment. These differences were significant between Busambuli-*Heinsenia*, Busambuli-Kisere, Isiukhu-*Heinsenia* and Yala-*Heinsenia* (p < 0.01). The analysis of wet and dry seasons did not show significant differences.

In the first wet season the numbers of individuals per study site ranged from 64 to 383, allocated from 14 to 24 species (Table 8). Most species were found on *Teclea* at Colobus Trail and at Busambuli River, least in the Kisere Forest. The beetles were most abundant at the Yala fragment and at Busambuli River. The rarefaction curve revealed expected species numbers between 13 and 17 for the smallest common random sample of 66 individuals (Fig. 24). Most species were expected for *Heinsenia* at Colobus Trail, least for the Kisere Forest. Differences between the study sites were relatively low, but the proportion of singletons differed clearly, ranging from 9 % in the Yala fragment to 53 % on *Heinsenia* at Colobus Trail. The dominance of single species was quite similar at all sites, only the value at Colobus Trail was somewhat higher.

The results for the second wet season were similar to those of the first wet season. The numbers of individuals ranged from 92 to 433 and they were allocated to 15−25 species (Table 8). Most species were found at Isiukhu River and Busambuli River. The fungivore beetles were again most abundant in the Yala fragment and at Busambuli River. The comparison of the rarefaction curves showed that the site at Isiukhu River with 19 expected species is supposed to be more diverse than the other sites (14−16 species). The curve was much steeper than the others ones (Fig. 24) and also the dominance of species was much lower than at the other sites. The comparison of species numbers for the common random sample (n_{ind} = 100) between both wet seasons did not show any significant differences between the sites studied, though the numbers of species at Isiukhu River were again the highest.

The results for the dry seasons were similar to those of the wet season. During the first dry season the number of species ranged from 13 on *Heinsenia* at Colobus Trail to 26 in the Yala fragment (Table 8). Remarkable were the differences in the abundances, ranging from 45 on *Heinsenia* at Colobus Trail to 349 in the Yala fragment. The rarefaction curve revealed expected species numbers between ten and 14 for the smallest common random sample of 31 individuals (Fig. 24). Most species were expected for Colobus Trail and Kisere Forest, least at Isiukhu River. So, differences between the study sites were again relatively low. Differences between the proportions of singletons were high, since 47 % singletons were found at Colobus Trail and no singletons at Isiukhu River. At the latter site one species of Corylophidae was very abundant, leading to the highest value for dominance of species.

In the second dry season the numbers of individuals per study site ranged from 28 on *Heinsenia* at Colobus Trail to 379 at Busambuli River, allocated to 10−26 species (Table 8). Most species were found at Isiukhu River and Busambuli River, least on *Teclea* and *Heinsenia* at Colobus Trail. Most abundant were the mycetophagous beetles in the Yala fragment and at Busambuli River. The rarefaction curve revealed expected species numbers between eight and twelve (Fig. 24) and, contrary to the first

Table 8: Species diversity of mycetophagous beetles. S_{Obs} = Species observed, N = number of individuals, Singletons = species represented in the sample with only one specimen, ACE, ICE, Chao 1 = richness estimators, D = Simpson's Diversity Index and J' = Shannon's evenness index.

| X.2001	bus	isi	yal	col	hein	kis
S_{obs}	24	18	23	24	17	14
N	363	146	383	192	64	80
Singletons	3	5	2	10	9	5
ACE	25	23	23	38	31	19
ICE	29	27	27	41	29	23
Chao 1	25	22	23	32	36	20
Simpson (D)	0.12	0.10	0.14	0.23	0.11	0.12
Evenness (J')	0.77	0.84	0.76	0.65	0.84	0.85
I.2002	bus	isi	yal	col	hein	kis
S_{obs}	22	22	26	17	13	17
N	308	325	349	46	45	114
Singletons	5	0	9	8	6	4
ACE	26	23	43	24	21	19
ICE	31	24	38	33	20	21
Chao 1	30	26	29	30	17	17
Simpson (D)	0.13	0.27	0.11	0.15	0.12	0.08
Evenness (J')	0.77	0.63	0.77	0.82	0.85	0.91
X.2002	bus	isi	yal	col	hein	kis
S_{obs}	25	23	21	20	15	16
N	433	120	312	117	93	119
Singletons	6	6	6	8	4	3
ACE	30	28	28	28	19	17
ICE	29	34	31	43	29	49
Chao 1	26	23	39	22	21	21
Simpson (D)	0.13	0.07	0.12	0.18	0.14	0.16
Evenness (J')	0.75	0.88	0.79	0.73	0.82	0.78
I.2003	bus	isi	yal	col	hein	kis
S_{obs}	23	26	19	10	12	15
N	379	183	254	48	28	76
Singletons	4	7	7	4	4	6
ACE	25	31	29	13	15	21
ICE	27	50	27	24	24	25
Chao 1	27	29	26	12	13	23
Simpson (D)	0.14	0.17	0.12	0.42	0.09	0.15
Evenness (J')	0.76	0.72	0.77	0.60	0.92	0.81
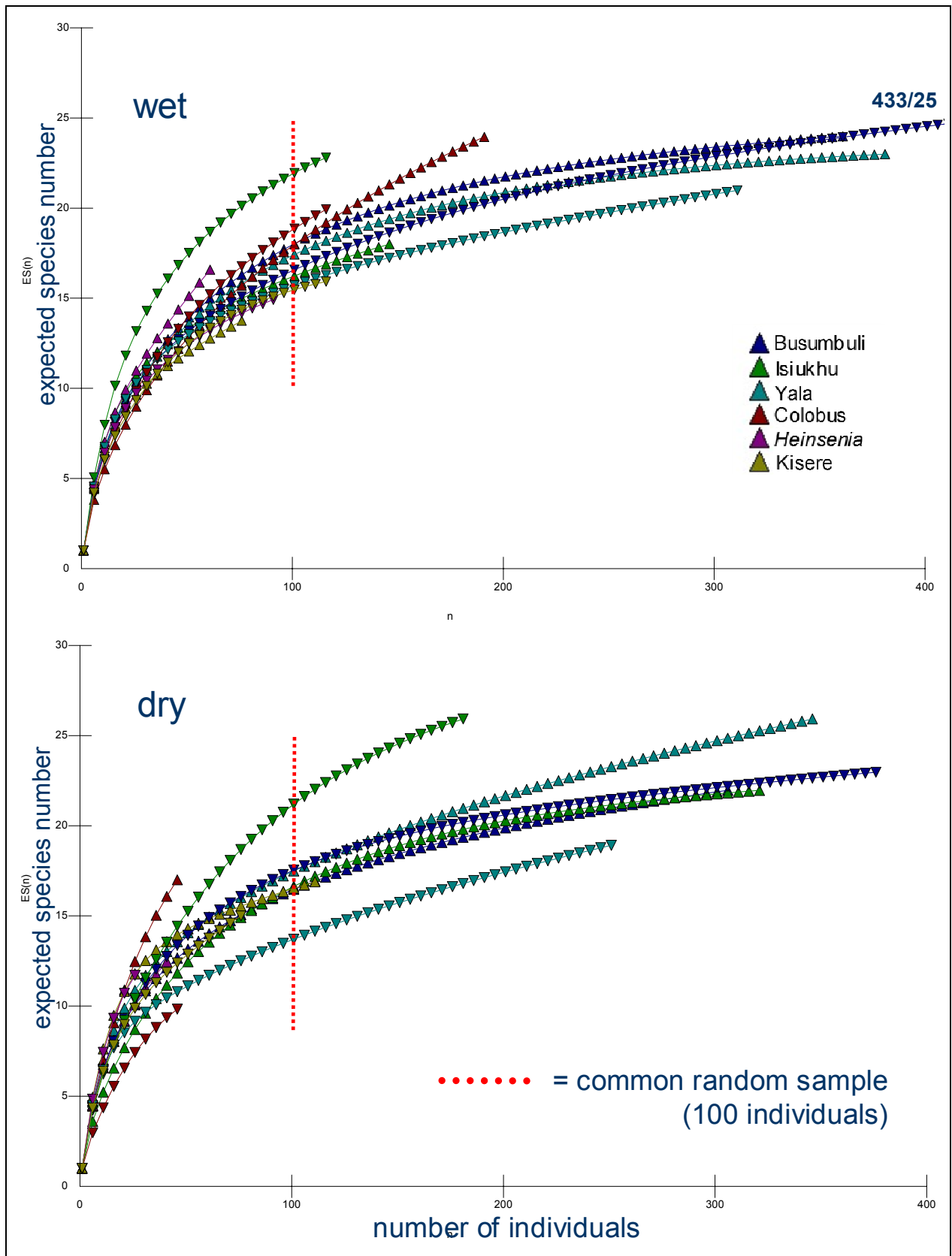
Fig. 24: Rarefaction plot of both wet seasons (top) and both dry seasons (bottom) for mycetophagous beetles; ▲= X.2001,I.2002; ▼=X.2002,I.2003.
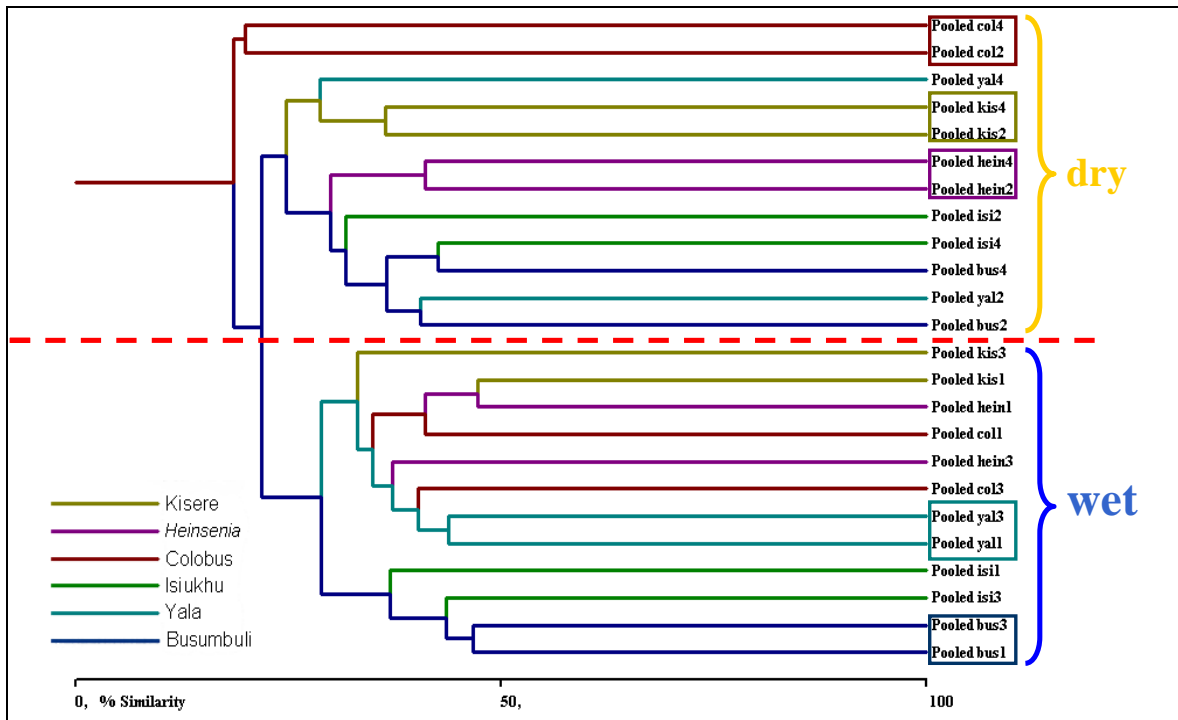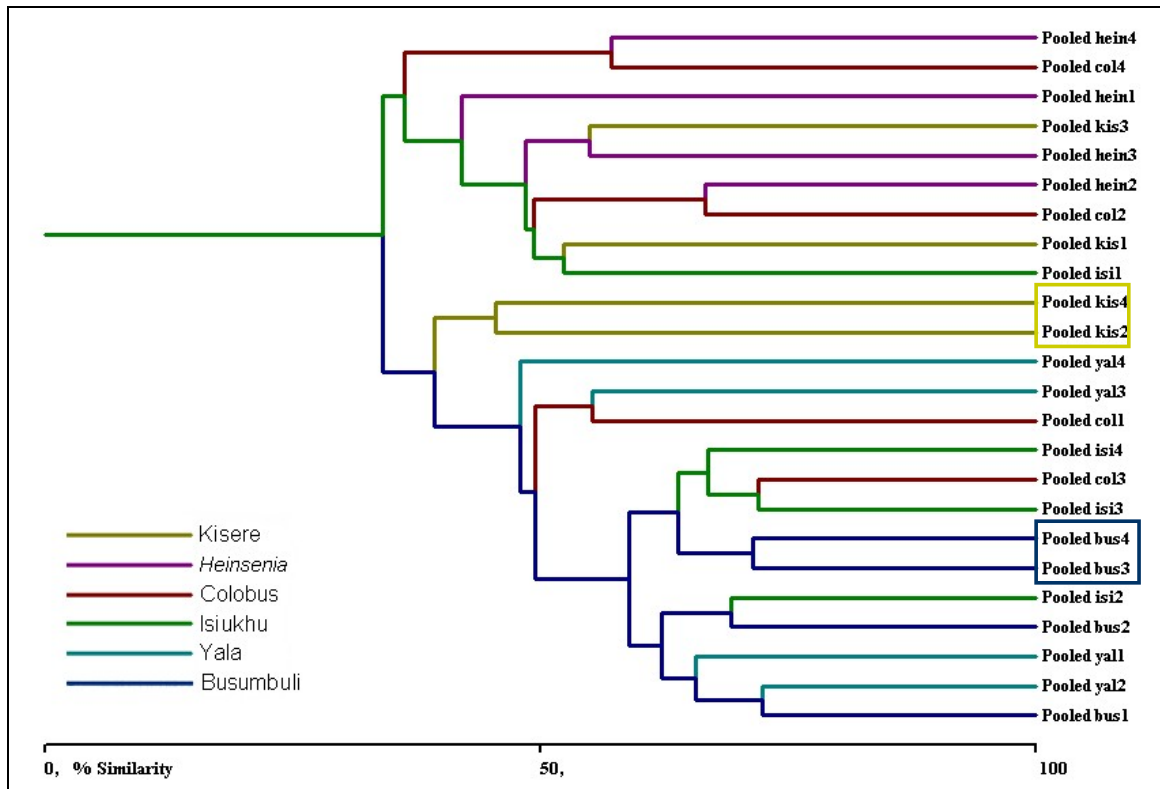
Fig. 25: Cluster analysis for mycetophagous beetles. Each collecting unit is represented by four samples (1 = X.2001 (wet), 2 = I.2002 (dry), 3 = X.2002 (wet), 4 = I.2003 (dry)). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.
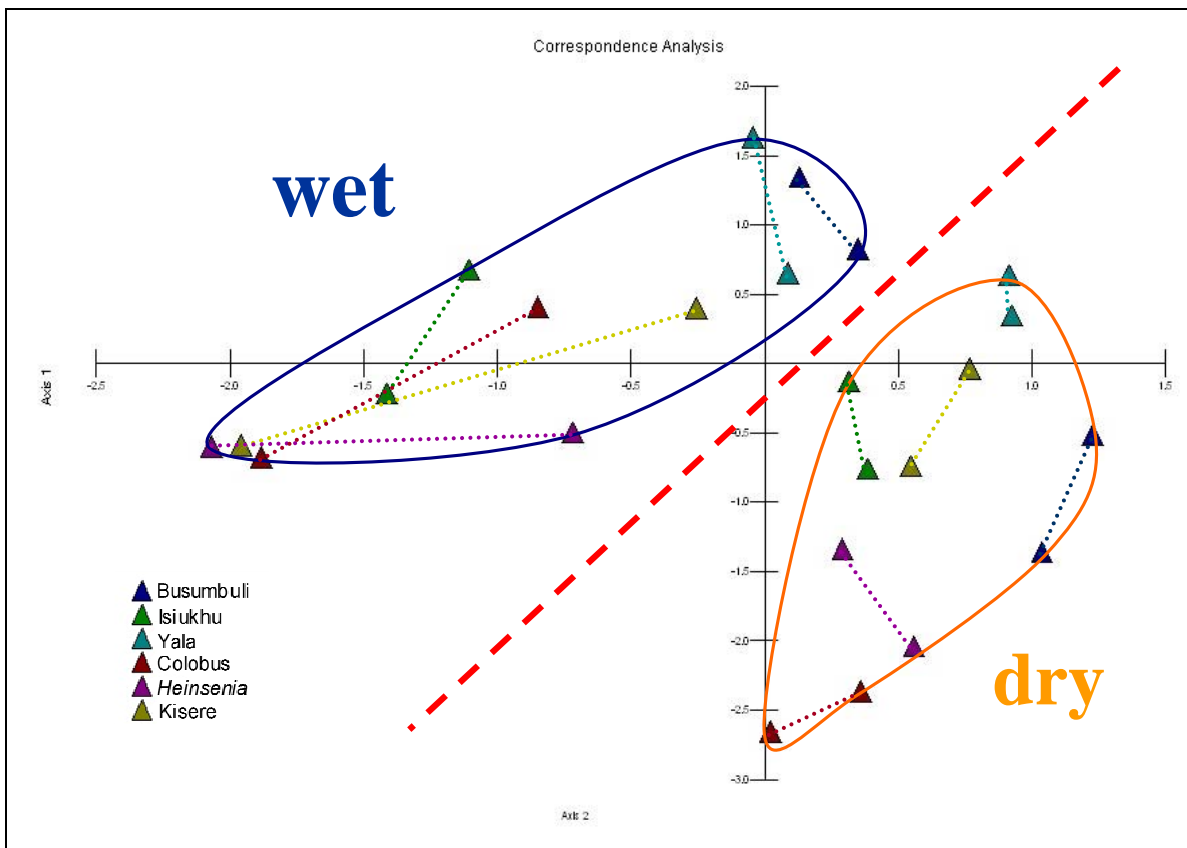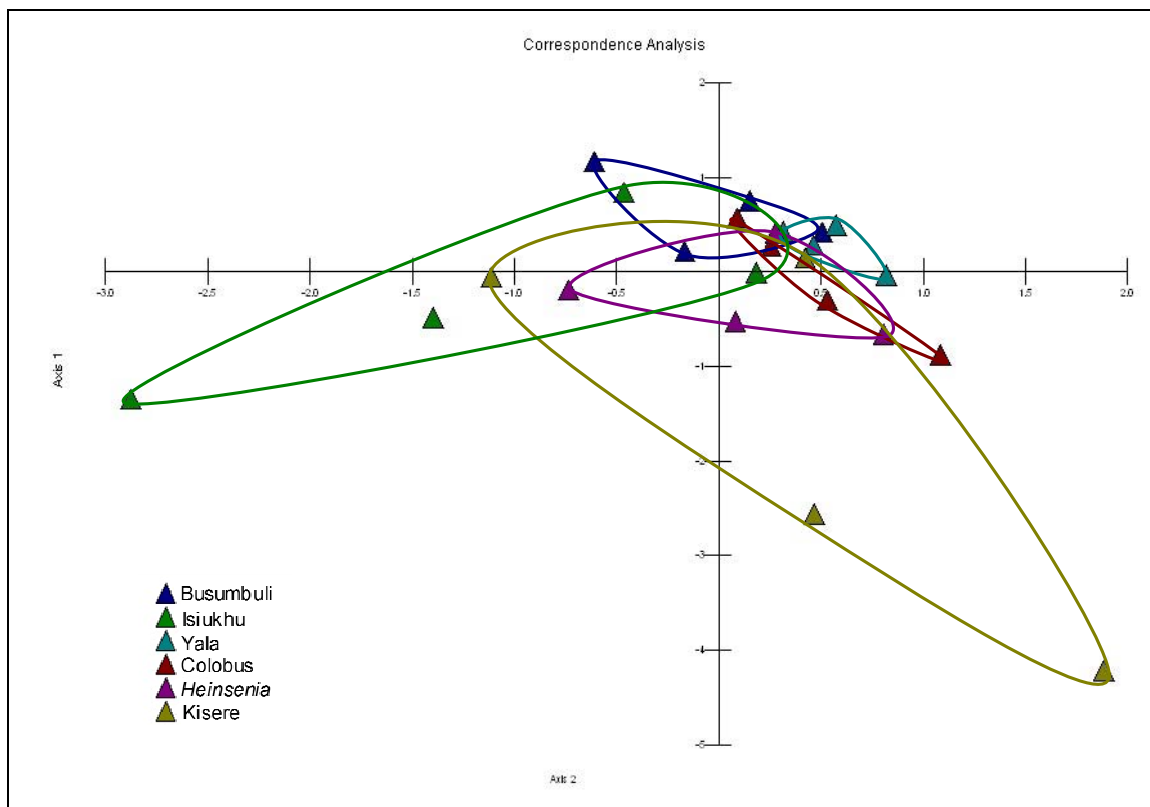

Fig. 26: Correspondence analysis for mycetophagous beetles. Each collecting unit is represented by four samples (two wet and two dry seasons). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.

dry season, most of the species were now expected at Isiukhu River and least for Colobus Trail. Because one single species of Corylophidae was very dominant, evenness was very low at the latter site. The comparison of species numbers for the common random sample (n_{ind} = 100) between both dry seasons did not show any significant differences between the sites studied.

The cluster analysis showed two main clusters, however, a distinct pattern was not recognisable (Fig. 25). Similarities were generally high, but neither between assemblages sampled at the same site, nor between assemblages sampled in the same season. Influence of forest type or seasonality was very low, only two samples from Kisere Forest and Busambuli River built a cluster each. A clear tree specific pattern did not exist. The correspondence analysis showed very homogenously distributed samples (Fig. 26). All samples, within each site and between sites, were plotted closely together with the exception of Isiukhu and Kisere which had two outliers each. Differences between forest types, seasons or tree species were not very high and did not seem to have a high influence on the distribution of samples.

Faunal overlap within seasons

Faunal overlap was generally low. In X.2001 values ranged from 16 to 40 %, with the highest value found within the collecting unit of Colobus Trail (Fig. 27). In I.2002 values varied between 16 to 42 %, with the highest values found within the site at Busambuli River (42 %) and the Yala fragment (41 %). The same pattern was found in X.2002, where values were ranging from 14 to 45 % and faunal composition was most similar within the site at Busambuli River (43 %), the Yala fragment (45 %), on *Heinsenia* at Colobus Trail (41 %), between *Heinsenia*-Yala (43 %) and between Yala-Colobus (42 %). In I.2003 high similarities were found within the site at Busambuli River (56 %), Colobus Trail (58 %) and between Colobus-Kisere (42 %); other values were ranging from five to 39 %.

Faunal overlap between seasons

Comparisons between the seasons showed also no peculiarities. The total range of faunal overlap was from seven to 44 %, with the latter found between both wet seasons and between trees of *Teclea* and *Heinsenia* at Colobus Trail (col1-hein3). Most of the values between sites and seasons ranged from ten to 30 % and faunal overlap was only

higher within the sites at Busambuli River (up to 41 %), the Yala fragment (up to 42 %) and Colobus Trail (up to 40 %).

Myc	bs1	isi1	yal1	col1	hei1	kis1	bs2	isi2	yal2	col2	hei2	kis2	bs3	isi3	yal3	col3	hei3	kis3	bs4	isi4	yal4	col4	hei4	kis4
bus1	0.33																							<25
isi1	0.20	0.34																						25<40
yal1	0.38	0.21	0.38																					40<55
col1	0.23	0.17	0.29	0.40																				55<70
hein1	0.30	0.21	0.36	0.28	0.37																			≥70
kis1	0.25	0.16	0.30	0.23	0.28	0.29																		
bus2	0.40	0.19	0.37	0.21	0.28	0.28	0.42																	
isi2	0.25	0.24	0.28	0.16	0.22	0.21	0.29	0.27																
yal2	0.36	0.21	0.41	0.30	0.26	0.26	0.38	0.31	0.41															
col2	0.23	0.17	0.21	0.14	0.16	0.17	0.25	0.17	0.22	0.25														
hein2	0.30	0.16	0.36	0.19	0.31	0.26	0.30	0.22	0.27	0.18	0.27													
kis2	0.24	0.15	0.24	0.23	0.18	0.20	0.20	0.18	0.25	0.16	0.21	0.16												
bus3	0.34	0.21	0.39	0.30	0.33	0.31	0.41	0.31	0.40	0.14	0.30	0.21	0.43											
isi3	0.22	0.21	0.26	0.22	0.20	0.20	0.23	0.25	0.27	0.18	0.21	0.20	0.26	0.17										
yal3	0.31	0.16	0.40	0.40	0.30	0.25	0.27	0.24	0.42	0.12	0.27	0.25	0.38	0.25	0.45									
col3	0.31	0.20	0.37	0.40	0.31	0.29	0.29	0.22	0.36	0.15	0.28	0.26	0.38	0.24	0.42	0.38								
hein3	0.24	0.17	0.30	0.44	0.29	0.21	0.17	0.17	0.30	0.10	0.20	0.23	0.30	0.22	0.43	0.42	0.41							
kis3	0.16	0.12	0.18	0.30	0.16	0.26	0.12	0.12	0.19	0.10	0.12	0.15	0.18	0.14	0.25	0.26	0.30	0.33						
bus4	0.27	0.28	0.23	0.10	0.11	0.10	0.33	0.34	0.28	0.17	0.15	0.12	0.28	0.21	0.14	0.12	0.07	0.08	0.56					
isi4	0.19	0.33	0.20	0.20	0.13	0.13	0.17	0.27	0.23	0.15	0.14	0.16	0.21	0.24	0.18	0.21	0.20	0.16	0.39	0.36				
yal4	0.35	0.15	0.36	0.18	0.24	0.21	0.33	0.24	0.37	0.18	0.28	0.20	0.31	0.19	0.35	0.29	0.22	0.12	0.20	0.11	0.37			
col4	0.26	0.21	0.19	0.19	0.11	0.19	0.31	0.18	0.25	0.37	0.14	0.17	0.17	0.21	0.10	0.18	0.11	0.16	0.27	0.24	0.14	0.58		
hein4	0.16	0.13	0.17	0.15	0.16	0.15	0.17	0.13	0.13	0.15	0.15	0.12	0.15	0.12	0.12	0.15	0.13	0.10	0.13	0.12	0.11	0.20	0.05	
kis4	0.22	0.20	0.19	0.15	0.14	0.21	0.26	0.24	0.22	0.28	0.16	0.17	0.20	0.21	0.12	0.17	0.12	0.14	0.24	0.21	0.14	0.42	0.18	0.33

Fig. 27: Faunal overlap of mycetophagous beetles (4578 ind./54 ssp.) within and among study sites and seasons calculated with the Morisita-Horn Index. Numbers added to the abbreviations of the study sites represent the seasons: 1 = X.2001, 2 = I.2002; 3 = X.2002; 4 = I.2003. Bus, isi, yal and col = *Teclea nobilis*, hein and kis = *Heinsenia diervilleoides*.

3.2.3.3. Chrysomelidae

The samples from October 2001 to January 2003 revealed 2565 phytophagous beetles allocated to 134 species. This group consists of Alticinae (1886 individuals, 47 species), Cassidinae (16/4), Chrysomelinae (2/2), Criocerinae (5/3), Cryptocephalinae (2/2), Eumolpinae (270/33), Galerucinae (365/37), Hispinae (15/5) and Zeugophorinae (4/1). The species accumulation curve (Fig. 19) did not reach a plateau, i.e. many further species could be expected in the forest. The mean species numbers at Busambuli River, Isiukhu River and in the Yala fragment were higher than on *Heinsenia* at Colobus Trail and Kisere Forest. These differences were significant (p < 0.01) and, as the post hoc test showed, mean numbers of species on *Teclea* at Colobus Trail were also significantly higher than on *Heinsenia* at the same site (p < 0.01). The analysis of wet and dry seasons showed no significant differences for species numbers, but leaf beetles were significantly more abundant in the dry seasons (p < 0.001).

In the first wet season the numbers of individuals per study site ranged from 31 to 130, allocated to 12−39 species (Table 9). Most species and individuals were found on *Teclea* at Colobus Trail, along the Isiukhu River and in the Yala fragment, least on *Heinsenia* at Colobus Trail and Kisere Forest. The rarefaction curve revealed expected numbers of species between 12 and 20 for the smallest common random sample of 36 individuals (Fig. 28). Remarkable were the steep courses of all curves in the rarefaction plot, representing the high diversity of leaf beetles. Differences between the study sites were not very high, except the collecting unit of *Heinsenia* at Colobus Trail, where only twelve species were present (other sites: 18−20 species). The proportion of singletons was very high, ranging from 46 % up to 72 % in the Kisere fragment. Dominance of single species was generally low and only slightly higher for the collecting unit of *Heinsenia* at Colobus Trail.

The results of the second wet season were very similar to those of the first wet season. The number of individuals ranged from 37 to 117, allocated to 17−37 species (Table 9). Remarkable were the low numbers of species and individuals for Colobus Trail, because leaf beetles were most abundant and species rich at this site in the first wet season. Most species were found at Busambuli River and Isiukhu River where, including the Yala fragment, the leaf beetle fauna was most abundant. For the smallest common random sample, 20 species were expected at Kisere Forest, shown in the rarefaction curve (Fig. 28), thus, it is supposed to be the most diverse site. Least of all species numbers, namely 14, were expected for both collecting units at Colobus Trail. The proportion of singletons was again high, as well as the evenness. The comparison of species numbers for the common random sample between both wet seasons did not show any significant differences between the sites studied.

Similar species numbers, but generally more leaf beetles were found during the dry seasons. The species numbers ranged from 12 on *Heinsenia* at Colobus Trail to 35 in the Yala fragment, where beetles were also most abundant (Table 9). Remarkable was the low proportion of singletons at Busambuli River, namely 30 % (other sites: 42−61 %), and dominance of single species was higher at all sites than in both wet seasons. The highest value was found on *Heinsenia* at Colobus Trail, where the 100 specimens collected were not equally distributed, since two species of Alticinae were very dominant with 83 individuals. The rarefaction curve revealed expected species numbers between ten on *Heinsenia* at Colobus Trail and 23 at Isiukhu River for the smallest common random sample of 66 individuals (Fig. 28). The remaining sites showed similar numbers of 18 to 19 species.

The most species during the second dry season were collected at Busambuli River Trail (38 ssp, Table 9). The species numbers at the other study sites ranged from 16 to 32. Most abundant were the Chrysomelidae in the Yala fragment. Dominance of species was also higher than in both wet seasons, especially at Busambuli River, where more than half of the individuals belonged to only three species of Alticinae. On *Heinsenia* at Colobus Trail and in the Kisere Forest, the same species of Alticinae was very

Table 9: Species diversity of leaf beetles. S_{Obs} = Species observed, N = number of individuals, Singletons = species represented in the sample with only one specimen, ACE, ICE, Chao 1 = richness estimators, D = Simpson's Diversity Index and J' = Shannon's evenness index.

X.2001	bus	isi	yal	col	hein	kis
S_{obs}	32	36	35	39	12	18
N	85	130	106	130	37	31
Singletons	15	17	20	18	8	13
ACE	50	62	72	63	34	56
ICE	52	58	93	89	33	71
Chao 1	45	56	59	58	44	45
Simpson (D)	0.05	0.05	0.11	0.06	0.18	0.07
Evenness (J')	0.90	0.87	0.80	0.86	0.79	0.91
I.2002	bus	isi	yal	col	hein	kis
S_{obs}	23	28	35	23	12	19
N	108	102	220	102	100	67
Singletons	7	14	18	14	5	10
ACE	28	52	74	67	16	36
ICE	31	52	74	75	20	71
Chao 1	25	52	61	54	15	27
Simpson (D)	0.17	0.08	0.16	0.16	0.40	0.16
Evenness (J')	0.76	0.84	0.68	0.73	0.54	0.76
X.2002	bus	isi	yal	col	hein	kis
S_{obs}	37	35	30	19	17	20
N	117	107	117	63	49	37
Singletons	19	22	17	10	10	11
ACE	66	92	65	33	41	34
ICE	82	80	63	34	37	32
Chao 1	56	93	76	28	33	28
Simpson (D)	0.11	0.06	0.08	0.15	0.11	0.05
Evenness (J')	0.80	0.85	0.83	0.78	0.84	0.94
I.2003	bus	isi	yal	col	hein	kis
S_{obs}	38	32	27	23	16	19
N	227	151	228	116	63	72
Singletons	18	14	14	12	8	12
ACE	63	55	55	47	23	48
ICE	71	53	50	55	43	64
Chao 1	64	42	50	46	22	36
Simpson (D)	0.15	0.11	0.15	0.15	0.35	0.28
Evenness (J')	0.70	0.78	0.70	0.74	0.63	0.66
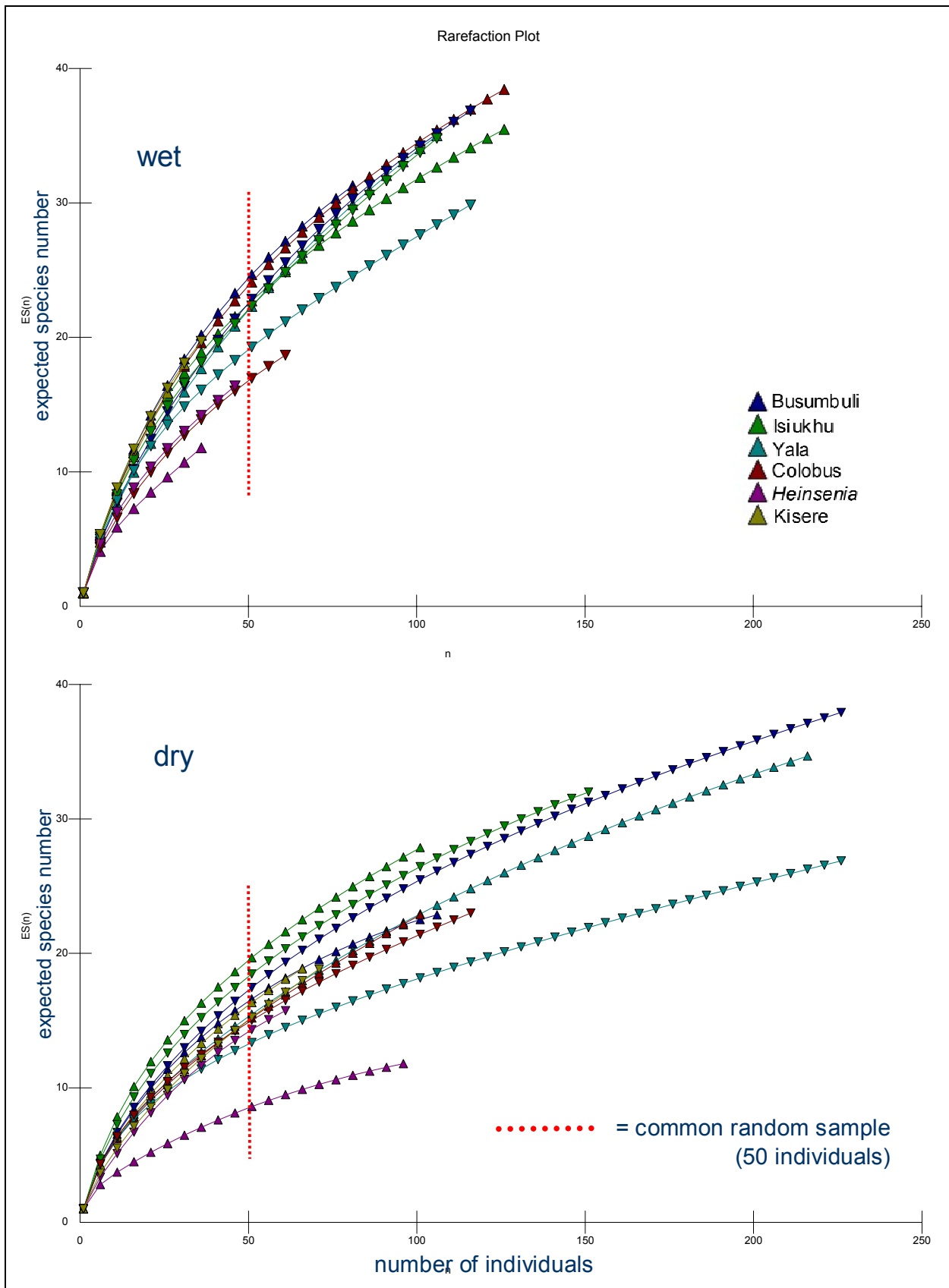
Fig. 28: Rarefaction plot of both wet seasons (top) and both dry seasons (bottom) for leaf beetles; ▲= X.2001,I.2002; ▼=X.2002,I.2003.
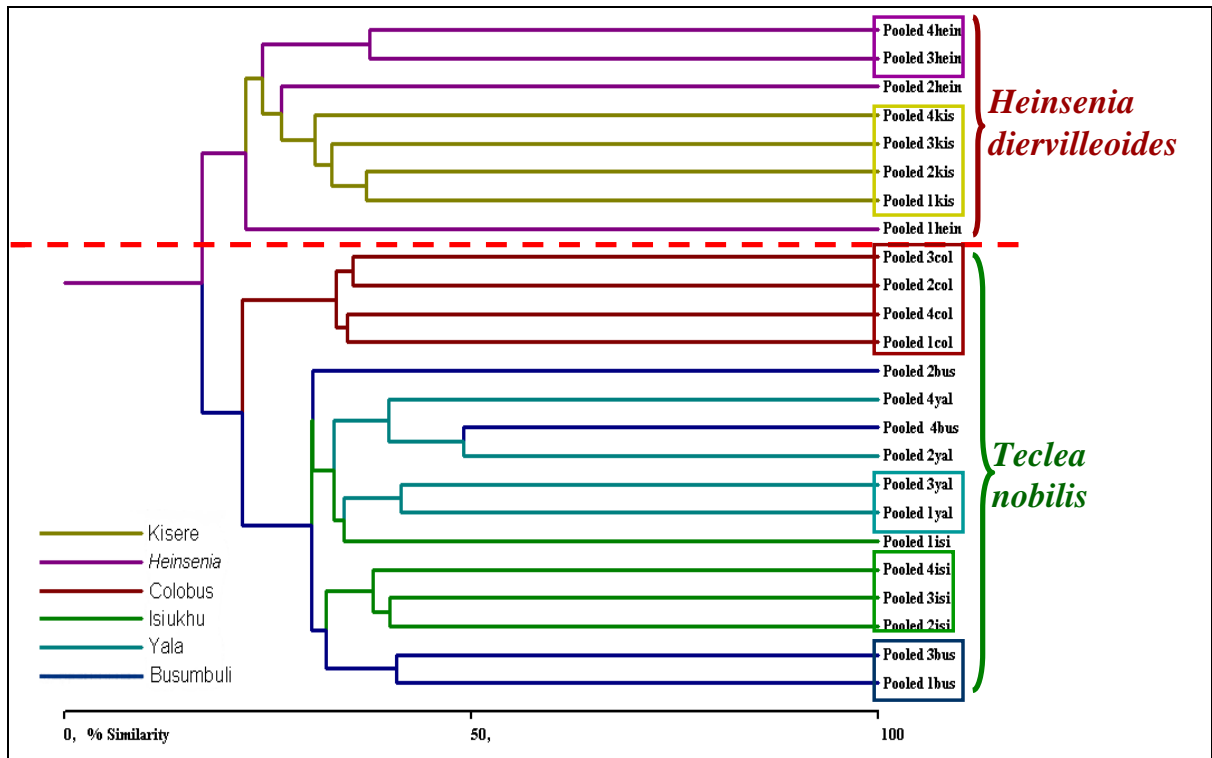
Fig. 29: Cluster analysis for Chrysomelidae. Each collecting unit is coloured differently and represented by four samples (1 = X.2001 (wet), 2 = I.2002 (dry), 3 = X.2002 (wet), 4 = I.2003 (dry)). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.
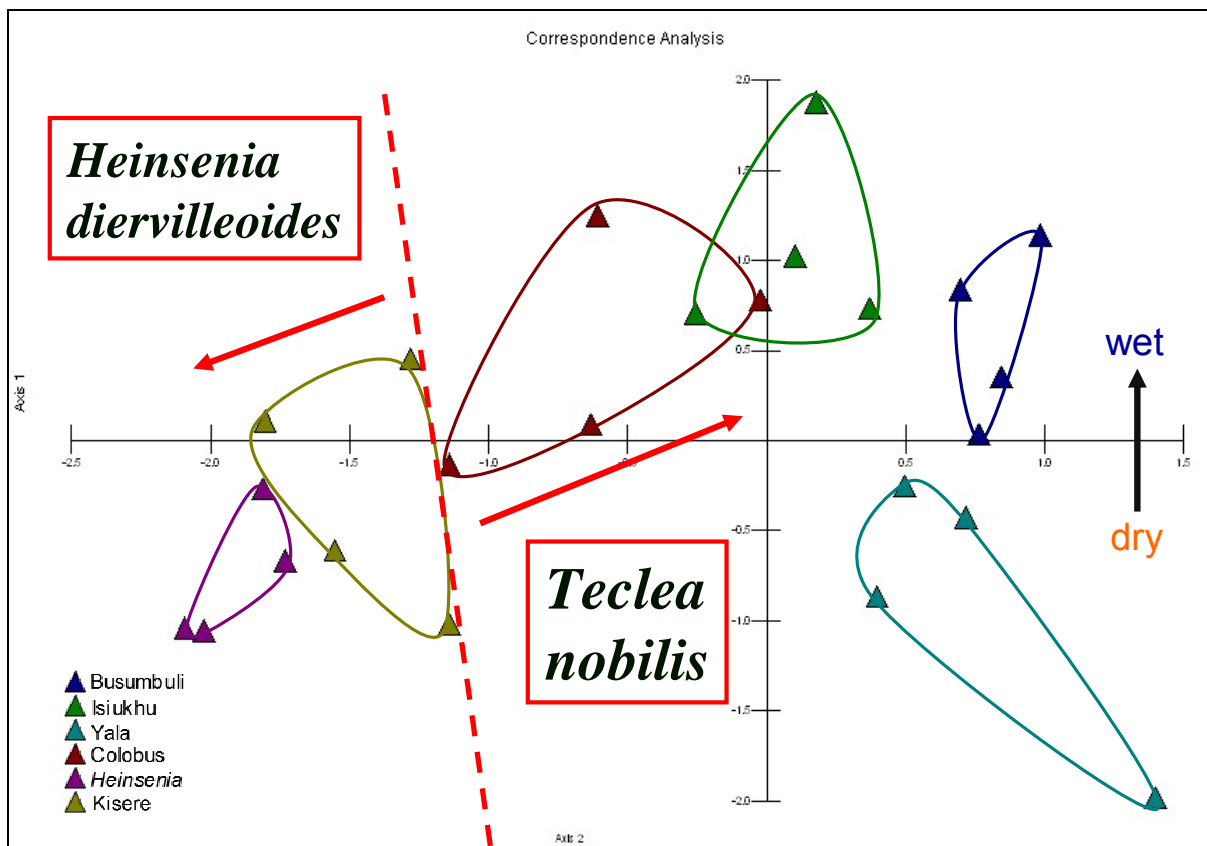
Fig. 30: Correspondence analysis for leaf beetles. Each collecting unit is represented by four samples (two wet and two dry seasons). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.

abundant. For the common random sample in the rarefaction curves least of all species were expected in Yala and most species were expected at Isiukhu River (Fig. 28). At the latter site the lowest proportion of singletons was recorded (44 %, other sites: 47−63 %). The differences in species numbers between the sites studied for the common random sample (n_{ind} = 50) between both dry seasons were significant, since the assemblages of Isiukhu River were more diverse than the assemblages on *Heinsenia* at Colobus Trail (p <0.05).

Similarities of the cluster analysis for the Chrysomelidae were generally low, but the results showed two distinct clusters for the two different tree species investigated (Fig. 29). Also impact of the forest type was high, since all four samples at each site for the collecting units of Colobus Trail and Kisere Forest built an exclusive cluster and this also applied, to a lower extent, to the samples of Isiukhu River, the Yala fragment, Busambuli River and the *Heinsenia* collecting units at Colobus Trail, where at least two samples of each site were very similar. The influence of tree species and forest type was also visible in the Correspondence Analysis (Fig. 30). Both tree species could be well separated and also the samples of each site showed clear differences. In each case both samples of the dry seasons were placed below the samples of the wet seasons, showing a gradient and influence of seasonality, respectively.

Faunal overlap within seasons

During the rainy seasons faunal overlap was low (Fig. 31). In X.2001 values ranged from only two to 51 % and high similarities were only recorded within the collecting unit in the Yala forest fragment (51 %) and within the *Heinsenia* collecting unit at Colobus Trail (47 %). In X.2002 values of faunal overlap varied between four and 56 % and high values occurred within the collecting unit at Busambuli River (56 %) and on *Heinsenia* at Colobus Trail (42 %). Within the dry season in I.2002 values were highest for the *Heinsenia* trees at Colobus Trail (86 %), Busambuli River (67 %) and between *Heinsenia* at Colobus Trail and Kisere Forest (62 %). Values were on average higher than during the wet seasons, ranging from 21 to 86 % and were only low between Busambuli-*Heinsenia* (Colobus) (5 %) and Busambuli-Kisere (8 %). The same results were achieved in the sampling session in I.2003, where values were highest within and between collecting units of *Heinsenia*, namely 79 % within Colobus Trail, 69 % within Kisere Forest and 73 % between Colobus-Kisere. Again, values for Busambuli-Kisere and Busambuli-*Heinsenia* (Colobus) were very low (4 and 8 % respectively), but within the collecting unit at Busambuli River faunal composition was similar to 74 %.

Faunal overlap between seasons

Faunal overlap was always high within the collecting unit of Busambuli River (31−65 %), the Yala fragment (34−54 %) and of *Heinsenia* at Colobus Trail (40−77 %). A high impact of tree species was shown, since values between the trees of *Heinsenia* and *Teclea* were very low (most of them lower than 10 % and maximal 22 %), but they were comparatively high (19−70 %) within and between the collecting units of *Heinsenia* at Colobus Trail and Kisere Forest. Between both dry seasons the faunal composition between both tree species showed higher similarities than between other seasons.

Chry	bs1	isi1	yal1	col1	hei1	kis1	bs2	isi2	yal2	col2	hei2	kis2	bs3	isi3	yal3	col3	hei3	kis3	bs4	isi4	yal4	col4	hei4	kis4
bus1	0.17																							<25
isi1	0.14	0.17																						25<40
yal1	0.26	0.11	0.51																					40<55
col1	0.12	0.08	0.13	0.20																				55<70
hein1	0.03	0.10	0.16	0.14	0.47																			≥70
kis1	0.02	0.07	0.07	0.09	0.29	0.14																		
bus2	0.31	0.14	0.37	0.21	0.06	0.03	0.67																	
isi2	0.20	0.19	0.26	0.22	0.24	0.13	0.40	0.44																
yal2	0.27	0.09	0.54	0.17	0.21	0.08	0.49	0.34	0.58															
col2	0.14	0.12	0.23	0.28	0.39	0.22	0.33	0.44	0.34	0.52														
hein2	0.01	0.06	0.12	0.19	0.56	0.32	0.05	0.34	0.21	0.58	0.86													
kis2	0.04	0.08	0.18	0.16	0.46	0.29	0.08	0.28	0.23	0.44	0.62	0.45												
bus3	0.33	0.13	0.35	0.23	0.05	0.05	0.55	0.37	0.42	0.29	0.03	0.07	0.56											
isi3	0.20	0.15	0.22	0.14	0.15	0.12	0.24	0.26	0.21	0.23	0.17	0.18	0.30	0.22										
yal3	0.24	0.10	0.38	0.14	0.10	0.06	0.37	0.25	0.38	0.20	0.07	0.11	0.36	0.21	0.36									
col3	0.20	0.09	0.22	0.20	0.06	0.04	0.34	0.24	0.26	0.23	0.05	0.07	0.37	0.17	0.21	0.23								
hein3	0.02	0.10	0.09	0.16	0.40	0.22	0.04	0.22	0.12	0.36	0.47	0.36	0.05	0.13	0.06	0.09	0.42							
kis3	0.03	0.07	0.05	0.11	0.19	0.14	0.04	0.12	0.05	0.17	0.22	0.20	0.04	0.10	0.06	0.05	0.21	0.08						
bus4	0.36	0.14	0.38	0.27	0.03	0.03	0.64	0.42	0.47	0.34	0.03	0.07	0.65	0.31	0.42	0.42	0.04	0.04	0.74					
isi4	0.23	0.15	0.23	0.19	0.11	0.09	0.35	0.33	0.25	0.32	0.21	0.19	0.38	0.31	0.25	0.27	0.15	0.10	0.44	0.36				
yal4	0.21	0.06	0.35	0.14	0.09	0.03	0.39	0.24	0.43	0.22	0.10	0.11	0.32	0.16	0.34	0.21	0.06	0.04	0.40	0.23	0.48			
col4	0.21	0.10	0.25	0.30	0.20	0.12	0.44	0.44	0.36	0.51	0.38	0.29	0.43	0.26	0.26	0.34	0.25	0.11	0.51	0.39	0.27	0.54		
hein4	0.02	0.04	0.13	0.18	0.41	0.21	0.04	0.31	0.21	0.52	0.77	0.52	0.02	0.13	0.05	0.06	0.43	0.18	0.04	0.22	0.12	0.39	0.79	
kis4	0.05	0.03	0.21	0.18	0.36	0.18	0.07	0.29	0.27	0.48	0.70	0.48	0.04	0.13	0.12	0.07	0.36	0.17	0.08	0.22	0.18	0.36	0.73	0.69

Fig. 31: Faunal overlap of Chrysomelidae (2565 ind./156 ssp.) within and among study sites and seasons calculated with the Morisita-Horn Index. Numbers added to the abbreviations of the study sites represent the seasons: 1 = X.2001, 2 = I.2002; 3 = X.2002; 4 = I.2003. Bus, isi, yal and col = *Teclea nobilis*, hein and kis = *Heinsenia diervilleoides*.

3.2.3.4. Weevils (Curculionidae and Apionidae)

The assemblages of all four sampling sessions between October 2001 and January 2003 revealed a total number of 5835 phytophagous weevils which were allocated to 128 species. This group consists of Curculionidae (2.676 individuals, 115 species) and Apionidae (3159/13). The species accumulation curve of the weevils (Fig. 19) also did not reach a plateau, i.e. many additional species probably live in the forest. Mean species numbers were highest for the collecting unit at Busambuli River and lowest for

the trees at Isiukhu River, on *Heinsenia* at Colobus Trail and in the Kisere Forest, but differences between these study sites were not significant. The analysis of wet and dry seasons showed that mean species numbers during wet seasons were higher than those during dry seasons, but these differences were also not significant.

In the first wet season the numbers of individuals per study site ranged from 114 to 563, allocated to 19−43 species (Table 10). The most species were found on *Teclea* at Colobus Trail and at Busambuli River, and least species in the Kisere Forest and along the Isiukhu River. Most abundant were the beetles on *Teclea* at Colobus Trail, where 563 weevils occurred (other study sites: 114−266 individuals). More than the half of them (= 57 %) belonged to a single species and hence, evenness was very low at this site. At Busambuli River and in Kisere Forest evenness was also low, since nearly half of all weevils collected at these sites belonged to one species only. The rarefaction curve revealed expected species numbers between 16 and 26 for the smallest common random sample of 116 individuals (Fig. 32). The least species were expected for the Kisere Forest and Isiukhu River, namely 16 and 19 respectively. Most species were expected for the Yala fragment and this site is supposed to be more diverse than the other sites. This was also shown by the lowest diversity index of all sites. The proportion of singletons was relatively low, ranging from 16 % in the Kisere Forest to 47 % at Busambuli River.

In the second wet season numbers of individuals ranged from 164 to 332, allocated to 21−36 species (Table 10). Although weevils were most abundant and species rich on the collecting unit of *Teclea* at Colobus Trail during the first season, least of all individuals and only a few species were found at this site in the second wet season. Less species were only found on the collecting unit of *Heinsenia* at Colobus Trail. The most individuals and species were collected at Busambuli River. The proportion of singletons was slightly higher than in the first wet season, ranging from 24 % on *Heinsenia* at Colobus Trail to 56 % at Busambuli Trail. The indices for dominance were comparable to those of the first wet season. The values were also quiet high, due to one or two species of Curculionidae or Apionidae were very dominant at each site studied. The rarefaction curve revealed expected species numbers between 18 and 22 (Fig. 32). The least species were expected at Kisere Forest, on *Heinsenia* at Colobus Trail and Isiukhu River, the most species were expected at Busambuli River. The comparison of species numbers for the common random sample between both wet seasons did not show any significant differences between the sites studied.

During the first dry season differences in species numbers between study sites were lower than during the wet season. Species numbers ranged from 21 to 26, where the least individuals were collected at Busambuli River and most individuals on *Heinsenia* at

Colobus Trail (Table 10), but diversity was rather similar at all sites. The proportion of singletons was low, ranging from 14 % in Kisere Forest to 42 % at Busambuli River and also diversity indices were relatively low, with the largest differences between Colobus Trail and Busambuli River.

Table 10: Species diversity of weevils. S_{Obs} = Species observed, N = number of individuals, Singletons = species represented in the sample with only one specimen, ACE, ICE, Chao 1 = richness estimators, D = Simpson's Diversity Index and J' = Shannon's evenness index.

| X.2001	bus	isi	yal	col	hein	kis
S_{obs}	34	19	27	43	22	19
N	266	114	123	563	122	225
Singletons	16	5	12	17	9	3
ACE	58	24	42	62	32	20
ICE	67	29	46	74	34	23
Chao 1	49	21	50	71	41	20
Simpson (D)	0.26	0.17	0.08	0.34	0.12	0.27
Evenness (J')	0.59	0.75	0.85	0.53	0.80	0.64
I.2002	bus	isi	yal	col	hein	kis
S_{obs}	24	25	26	24	23	21
N	88	232	256	248	440	205
Singletons	10	9	10	9	7	3
ACE	34	34	37	35	31	23
ICE	38	37	39	39	29	26
Chao 1	36	66	38	31	34	22
Simpson (D)	0.09	0.10	0.12	0.18	0.14	0.11
Evenness (J')	0.85	0.80	0.75	0.67	0.73	0.81
X.2002	bus	isi	yal	col	hein	kis
S_{obs}	36	24	30	22	21	23
N	275	239	332	164	207	251
Singletons	20	9	14	7	5	6
ACE	82	34	55	28	27	25
ICE	86	35	62	35	26	38
Chao 1	68	33	53	26	27	26
Simpson (D)	0.27	0.24	0.17	0.24	0.18	0.21
Evenness (J')	0.58	0.64	0.67	0.67	0.75	0.67
I.2003	bus	isi	yal	col	hein	kis
S_{obs}	26	23	22	20	22	25
N	312	183	289	205	213	283
Singletons	11	9	8	6	7	10
ACE	42	40	31	28	31	25
ICE	42	42	35	30	31	36
Chao 1	45	32	54	23	26	37
Simpson (D)	0.30	0.15	0.23	0.16	0.16	0.14
Evenness (J')	0.57	0.74	0.66	0.74	0.73	0.73
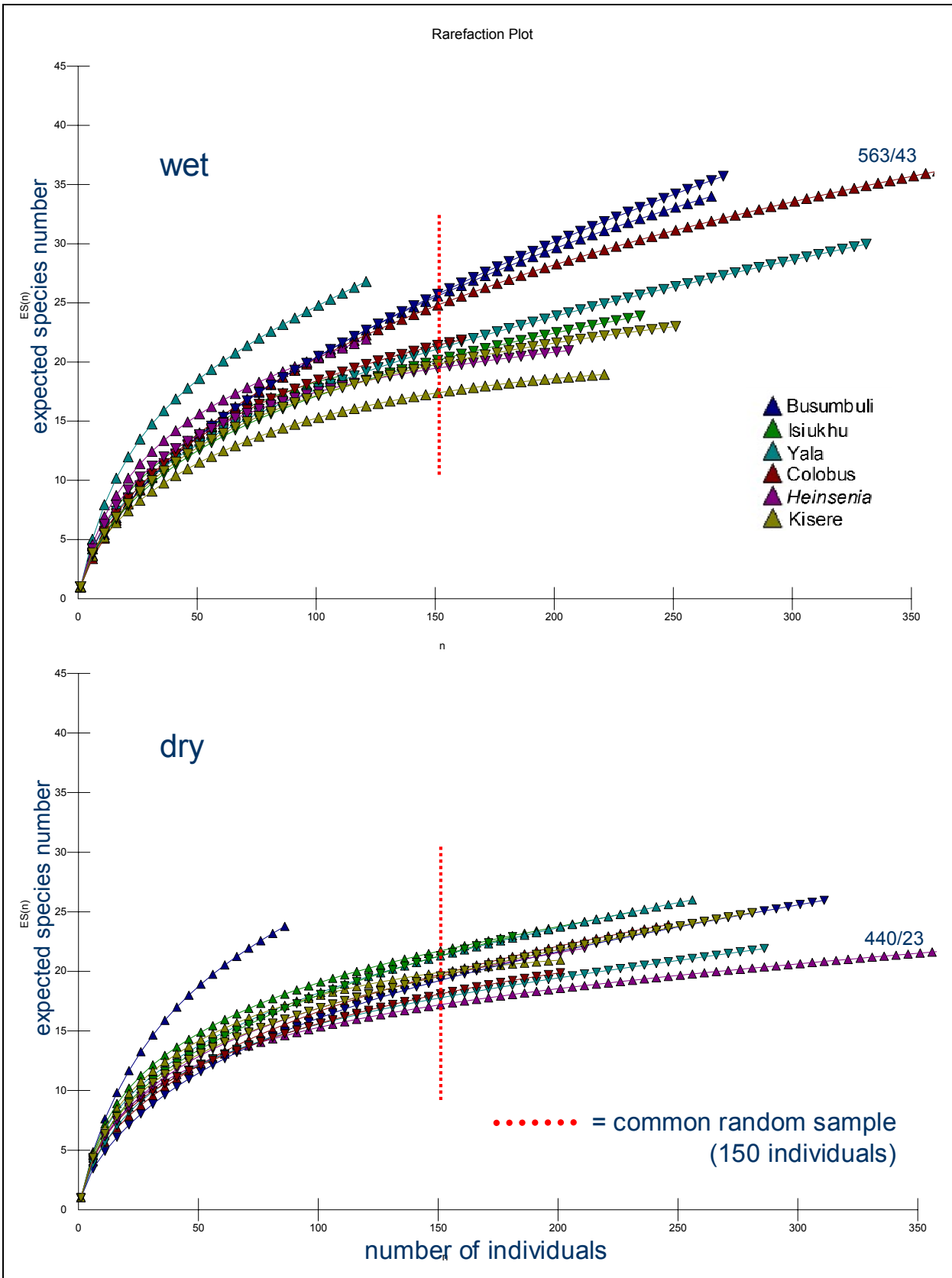
Fig. 32: Rarefaction plot of both wet seasons (top) and both dry seasons (bottom) for weevils; ▲= X.2001,I.2002; ▼=X.2002,I.2003.
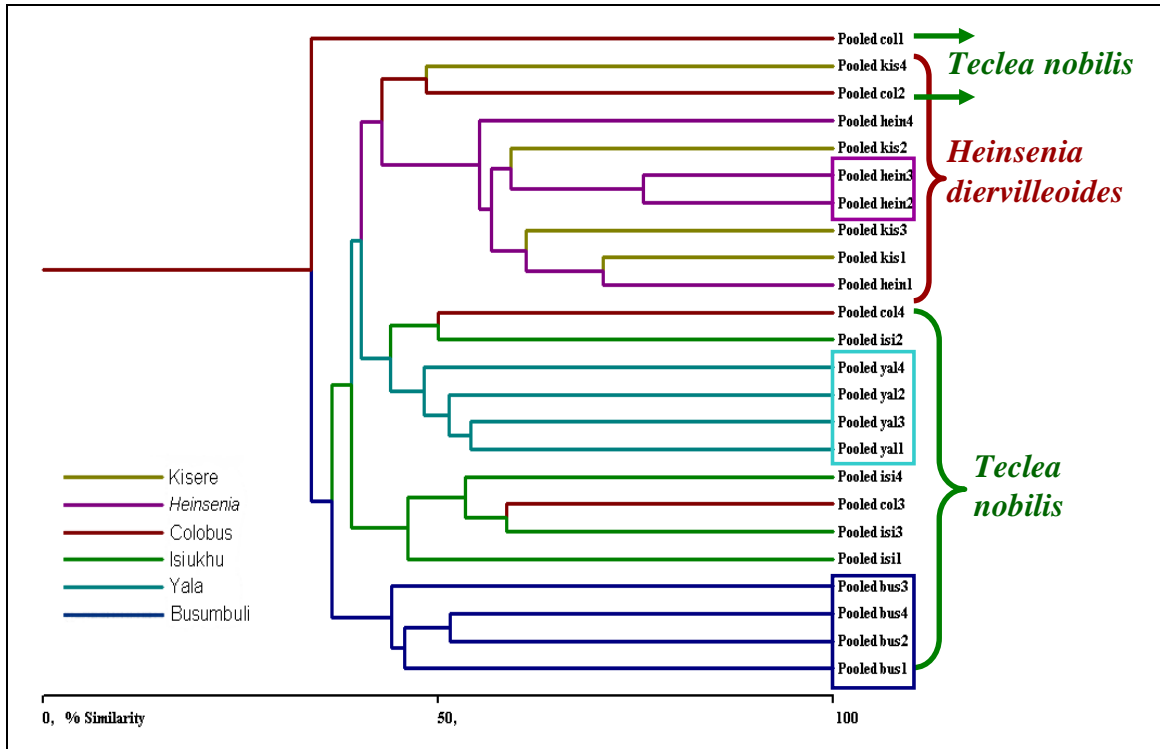
Fig. 33: Cluster analysis for Curculionidae and Apionidae. Each collecting unit is represented by four samples (two wet and two dry seasons). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.
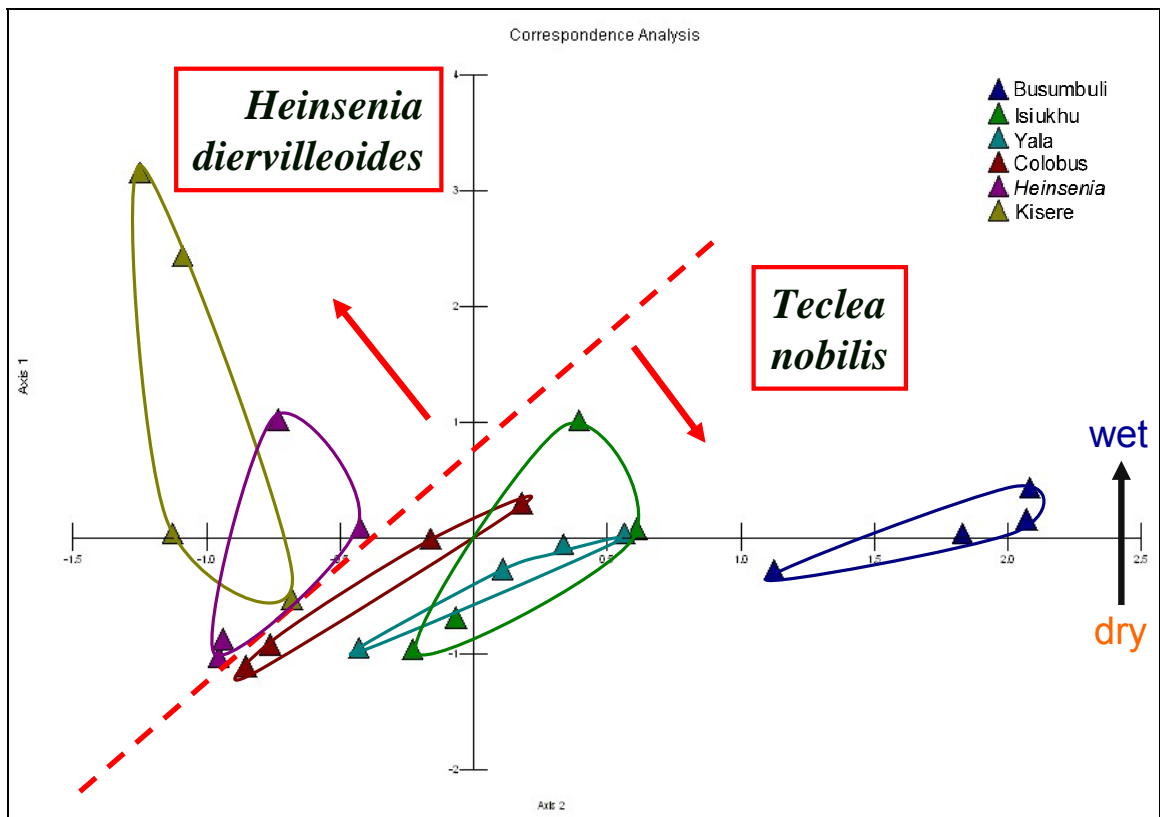
Fig. 34: Correspondence analysis for weevils. Each collecting unit is marked with different colours and represented by four samples (1 = X.2001 (wet), 2 = I.2002 (dry), 3 = X.2002 (wet), 4 = I.2003 (dry)). Bus, yal, isi, col = *Teclea nobilis* and kis, hein = *Heinsenia diervilleoides*.

During the second dry season numbers of individuals per study site ranged from 183 to 312, allocated to 20−26 species (Table 10). The most individuals and species occurred at Busambuli River. Expected numbers of species of the rarefaction curve were very similar, ranging from 15 to 17 (Fig. 32). The proportion of singletons was low, ranging from 30 % at Colobus Trail to 42 % at Busambuli River. Since more than a half of the weevils collected at Busambuli River belonged to a single species of Apionidae and one species of Curculionidae was very abundant in the Yala fragment, diversity indices of these sites were relatively high, while indices at the other sites were comparatively low. The comparison of species numbers for the smallest common random sample between both dry seasons did not show any significant differences between the sites studied, though the site at Busambuli River maintained considerably more species than the other sites.

The results of the cluster analysis showed two not very well separated clusters (Fig. 33), since the collecting units of *Heinsenia* and *Teclea* each built a cluster, but two samples of *Teclea*, both from Colobus Trail, lied within the *Heinsenia*-cluster. Similarities were high between the *Heinsenia* collecting units at Colobus Trail and Kisere Forest, indicating important influence of tree species on the distribution of some weevils. The forest type seemed to have even higher influence, since all four samples from Busambuli River and the Yala fragment each built strict clusters. Similarities were also high between samples at Isiukhu River and Colobus Trail and between Kisere and Colobus Trail, so that the distance of study sites might be also of importance. The results of the Correspondence Analysis showed similar results, since samples showed a clear influence of forest type, tree species and seasonality (Fig. 34).

Faunal overlap within seasons

Faunal overlap was generally high during wet and dry seasons (Fig. 35). In October 2001 values varied between eleven and 83 %, the latter value was calculated for the site at Colobus Trail. High similarity was also found for this site within the other seasons (62−71 %), as well as for the *Heinsenia* collecting unit at Colobus (77−80 %), Kisere Forest (59−75 %) and the Yala fragment (58−70 %). Faunal composition was also very similar between Colobus-*Heinsenia* (70−74 %) and Kisere-*Heinsenia* (54−72 %), indicating high influence of forest type and tree species on the presence and distribution of weevils. Least similarities were found between the trees at Busambuli River and the trees in the Kisere Forest and at Colobus Trail (both collecting units).

Faunal overlap between seasons

Similarities in faunal composition were high between both dry seasons and also between both wet seasons. High values were found within the collecting unit of *Teclea* at Colobus Trail (up to 71 %), within the collecting unit of *Heinsenia* (up to 73 %) and between both of them (up to 78 %, Fig. 35). Faunal overlap was also high between *Heinsenia* at Colobus Trail and *Heinsenia* in Kisere Forest (kis4-hein3) which was similar to 70 %. Least similarities were found between the trees at Busambuli River and the trees in Kisere Forest and at Colobus Trail (both collecting units).

Curc	bs1	isi1	yal1	col1	hei1	kis1	bs2	isi2	yal2	col2	hei2	kis2	bs3	isi3	yal3	col3	hei3	kis3	bs4	isi4	yal4	col4	hei4	kis4
bus1	0.58																							
isi1	0.35	0.43																						
yal1	0.34	0.32	0.44																					
col1	0.36	0.47	0.45	0.83																				
hein1	0.21	0.36	0.33	0.52	0.47																			
kis1	0.11	0.30	0.18	0.27	0.45	0.69																		
bus2	0.43	0.24	0.29	0.21	0.15	0.07	0.29																	
isi2	0.23	0.21	0.37	0.34	0.26	0.12	0.26	0.48																
yal2	0.25	0.24	0.44	0.47	0.34	0.14	0.27	0.56	0.62															
col2	0.16	0.18	0.32	0.35	0.32	0.13	0.22	0.50	0.54	0.71														
hein2	0.15	0.15	0.36	0.30	0.31	0.14	0.23	0.56	0.61	0.73	0.77													
kis2	0.13	0.18	0.30	0.28	0.38	0.31	0.18	0.45	0.47	0.63	0.65	0.59												
bus3	0.56	0.36	0.36	0.45	0.25	0.12	0.38	0.25	0.27	0.17	0.15	0.13	0.49											
isi3	0.40	0.43	0.42	0.68	0.41	0.20	0.27	0.37	0.44	0.32	0.30	0.25	0.46	0.58										
yal3	0.43	0.37	0.53	0.66	0.40	0.20	0.28	0.36	0.45	0.31	0.32	0.29	0.48	0.56	0.70									
col3	0.27	0.41	0.43	0.71	0.49	0.28	0.21	0.36	0.49	0.41	0.37	0.35	0.35	0.57	0.55	0.62								
hein3	0.30	0.43	0.49	0.78	0.56	0.30	0.20	0.41	0.54	0.48	0.46	0.44	0.38	0.62	0.66	0.70	0.80							
kis3	0.20	0.39	0.29	0.54	0.56	0.64	0.10	0.21	0.29	0.26	0.24	0.38	0.24	0.40	0.40	0.49	0.54	0.67						
bus4	0.64	0.34	0.36	0.47	0.25	0.11	0.43	0.27	0.32	0.21	0.18	0.16	0.60	0.48	0.51	0.37	0.40	0.24	0.67					
isi4	0.35	0.35	0.39	0.61	0.39	0.17	0.25	0.46	0.51	0.52	0.50	0.42	0.39	0.56	0.50	0.53	0.61	0.38	0.43	0.62				
yal4	0.30	0.35	0.42	0.67	0.42	0.18	0.23	0.40	0.52	0.41	0.40	0.32	0.37	0.59	0.54	0.60	0.64	0.40	0.41	0.57	0.58			
col4	0.16	0.17	0.37	0.37	0.33	0.13	0.26	0.52	0.60	0.70	0.71	0.59	0.19	0.35	0.33	0.45	0.49	0.25	0.24	0.48	0.46	0.71		
hein4	0.18	0.22	0.40	0.43	0.40	0.16	0.26	0.52	0.61	0.72	0.73	0.61	0.21	0.40	0.36	0.50	0.57	0.31	0.26	0.53	0.49	0.74	0.77	
kis4	0.25	0.34	0.46	0.61	0.49	0.25	0.23	0.51	0.60	0.67	0.67	0.59	0.30	0.53	0.51	0.60	0.70	0.45	0.32	0.64	0.63	0.65	0.72	0.75

Legend (shading): <25, 25<40, 40<55, 55<70, ≥70

Fig. 35: Faunal overlap of Curculionidae and Apionidae (5835 ind./128 ssp.) within and among study sites and seasons calculated with the Morisita-Horn Index. Numbers added to the abbreviations of the study sites representing the seasons: 1 = X.2001, 2 = I.2002; 3 = X.2002; 4 = I.2003. Bus, isi, yal and col = *Teclea nobilis*, hein and kis = *Heinsenia diervilleoides*.

4. Discussion

4.1. Distribution patterns and seasonality of non-beetle arthropods

One of the most important factors for the presence and distribution of arthropods in the tropics is probably humidity. Many scientists have worked on seasonality of tropical insects and therefore the existence of seasonal patterns is quite well known (Denlinger 1980, Wolda 1988, Basset & Kitching 1991, Wolda 1992a, Novotny & Basset 1998, Wagner 2001, Palacios-Vargas & Castano-Meneses 2003, Wagner 2003). Some works on the influence of seasonality upon arthropod communities in tropical forests show a much lower density of arthropods during dry seasons (Janzen & Schoener 1968, Frith & Frith 1985, Kitching & Arthur 1993). The results of the present work show that this does not apply for all groups of arthropods, since some are even more abundant in the dry season. But there is no general pattern for each season and total numbers of arthropods differ to large extent at each study site; e.g. on *Teclea* at Colobus Trail higher individual numbers could be found during the wet seasons, in Kisere Forest arthropods were more abundant during the dry seasons, while on *Heinsenia* at Colobus Trail arthropods were distributed without any visible pattern between seasons (Fig. 11, p. 32). Nevertheless, some of the arthropod groups show strong changes between dry and wet seasons.

Another factor which may influence the abundance of arthropods, is the height of the trees, volume and density of the canopy and thus, the numerous habitat structures, which are essential to sustain a diverse arboreal arthropod community (Lawton & Schröder 1977, Lawton 1983, Fowler 1985). Tree architecture, including the varying biomass of conspecific seedlings, saplings and trees, is a significant determinant of the richness of associated insect herbivores in tropical trees (e.g. Basset et al. 1999, Basset 2001a, Caraglio et al. 2001, Barrios 2003, Novotny et al. 2003) and differences in the volume of available habitats often correlate with resource availability (e.g. higher occurrence of young leaves, flowers and seeds in mature trees than in seedlings or saplings) (Basset et al. 2003). Not only do abiotic factors have an influence on the arthropod communities, but also biotic factors like predator-pray relationships. Since the impact of those factors differs between most of the taxa investigated to a large extent and distribution patterns are not generally valid for all arthropod groups, the possible causes for presence, abundance and distribution will be discussed for some major taxa in detail.

Formicidae

The most abundant group is the Formicidae with a total number of 36,203 individuals and a proportion of 14.85 % of all arthropods collected (Fig. 9, p. 31). They have a proportion of about 12 % during the wet seasons and of about 16 % during the dry seasons and this is a considerably lower proportion than found in other studies. Floren & Linsenmair (1994, see also Floren et al. 2002) found in their assemblages in a Malaysian rain forest a proportion of 44 to 66 % Formicidae, just as much as Adis (1988) and Guerrero (2003) found in forests in Central Amazon, namely about 60 % and 50 %, respectively. Therefore ants are the dominant group in the canopy fauna of tropical lowland rain forests. They are considered to be the key predators with a high impact on the abundance of less mobile, mainly holometabolous arthropods, while hemimetabolous highly mobile nymphs occur regularly and in large numbers in the trees (Floren et al. 2002, see also Halaj et al. 1997). In contrast to that, another suggestion is that ants are abundant to such an extent because they are not carnivores and feed on plants and homopteran exudates, but this is more probable in forests of the neotropics (Tobin 1991, 1994, Davidson 1997, 1998, Davidson et al. 2003). The high influence of ants on the abundance of phytophagous larvae or in general on phytophagous insects is also confirmed experimentally by Woodman & Price (1992). Probably as a strategy to avoid ants, most of the larvae of tropical leaf beetles are subterranean root-feeders, while most of the larvae in Central Europe are free-living and leaf-feeders (Novotny et al. 2003).

Nevertheless, it is reported that with increasing altitudes the abundance of ants and their ratio to other taxa decreases (Stork & Brendell 1990, Basset 2001b, Wagner 2002). This tendency can be explained by less effective food-gathering and slow development of their larvae due to colder temperatures, especially at nights (Brown 1973). Kakamega Forest is situated at an altitude of about 1600 m above sea level and therefore not a typical lowland rain forest and this might be an explanation for the partly low proportion of less than 10 % of ants collected at the study sites (see Appendices 2−5), during both wet and dry seasons. Similar results have been found by Watanabe & Ruaysoongnern (1989) in a rain forest in Thailand at an altitude of 800 m above sea level, where ants have a proportion of less than 16 % (cf. also Stork & Brendell 1990). Fewer individuals have been found only in lowland rain forest in Australia with proportions ranging from 3 to 5 % (Stork & Brendell 1990, Basset & Arthington 1992, Kitching & Arthur 1993).

Another aspect is the heterogeneous distribution of ants on trees, correlated with the presence of nests. If ants keep on swarming out of their nests during fogging, their proportion of the total number of arthropods collected can increase to a unusually large

extent, as it was for instance the case on one tree in the Kisere Forest (up to 31 %, see Appendix 3). The heterogeneous distribution is also shown by the high standard deviation of the total numbers (Appendix 2−5, see also Schulz & Wagner 2002). Nevertheless, it is not very surprising that none of the other taxa is negatively or significantly correlated with the abundance of ants, because obviously their numbers and hence their influence as predators is too low in this forest. Due to this fact and their heterogeneous distribution, statements on the differences between the study sites are not very useful and moreover these differences are not significant (except of I.2003, see Table 6, p. 42).

Diptera

Another very abundant group is Diptera with a total of 35,483 individuals and a proportion of 14.56 % (Fig. 9, p. 31). They are thought to use the canopies mainly for swarming at dusk and dawn (Haddow & Corbet 1961, Stork 1991), to seek the canopies for protection against predators or unfavourable climatic conditions, and using them as resting sites (Stork 1991, Didham 1997a). Therefore Diptera, which consists of numerous trophic groups such as predators, pollinators, fungivores and detritivores and which do not actively feed in the canopy, often have been classified as tourists (Stork 1991, Didham 1997a). However, Diptera definitely feed on the exudates of Homoptera (Stork 1987a). Didham (1997a) found in his study in a southern temperate rain forest that many species are specific to a different habitat type and few species are host specific and he suggested that Diptera play a much more important role in arboreal community interactions than implied by their designation as tourists in the canopy.

Differences between the sites studied are partly considerable, but not significant. On the other hand, the influence of seasonality is very high and the differences between seasons are highly significant ($p < 0.001$). The abundance of dipterans is clearly reduced during the dry seasons. The high amount of flies and nematocerous dipterans in the last dry season in January 2003 (N = 9906) can be explained by the sampling regime. The fogging event was conducted at the very beginning of the dry season, where the environment in some parts of the forest was still moist. Humidity, moist soil and for instance pools of water in tree holes or bromeliades are needed for the development of the larvae of dipterans. A general decreasing number of small, soft bodied and flying arthropods during dry seasons in tropical rain forests was also shown by Frith & Frith (1985) and Wolda (1978) who described this as a response to avoid dryness.

In contrast to these results, some small and soft bodied groups such as Psocoptera and Thysanoptera have been regularly more frequently collected during dry seasons (e.g. New et al. 1991 for Psocoptera, Wagner 2001 for Thysanoptera). This might be due to relatively high tolerance against drought, which was supposed by New et al. (1991), who also considered that heavy rainfalls in wet seasons might wash the psocids off the trees. This wash-out effect might be the reason for the unusual fluctuations of abundances, since at least the psocids were most abundant in each season at a different study site. For thrips it is also known that great shifts in their abundances occur from year to year (Roubik et al. 2003). Another suggestion is that they accumulate along a gradient of humidity, which is probably increased in the canopies during dry seasons (Wagner 2001). This is supported by a supposition different from New et al. (1991), namely that Psocoptera are known to require high humidity, often exceeding 65−70 % (Broadhead & Thornton 1955, Bowden et al. 1976). Nevertheless, for both groups no significant differences between wet and dry seasons could be found in this work. But since the species composition of these groups is totally unknown, one should note that the Psocoptera generally evolved different adaptations, since some species live mainly on ground or trunks, while others prefer the canopy (Broadhead & Wolda 1985) and also spatial migrations between ground and canopy are conceivable.

Parasitoid Hymenoptera

The next abundant group is parasitoid Hymenoptera (in this group Formicidae and Symphyta are excluded) with a proportion of 12.72 % (N = 30,997, Fig. 9, p. 31). This is an unusually high proportion, since in other studies much fewer Hymenoptera could be found (Floren & Linsenmair 1997, Wagner 1997 for lowland rain forest (but even higher proportions in montane rain forests), Marques et al. 2001, Guerrero et al. 2003). Most individuals of this group belong to the Ichneumonoidea and Chalcidoidea and these small insects are mostly parasitoids on eggs, larvae and small insects. Larger specimens of Apioidea and Vespoidea are quite rare and not well represented in the assemblages, since they are very good flyers and probably able to escape the fog right in time. Differences between dry and wet season are not remarkable, but the abundance of the Hymenoptera is positively correlated with the canopy volume ($p < 0.05$), a similar effect is found only in Coleoptera ($p < 0.05$) and (negatively correlated) in Formicidae ($p < 0.01$). A general correlation of the structure of a plant and density of arthropods is confirmed in many works (e.g. Lawton & Schröder 1977, Lawton 1983, Fowler 1985). An increased canopy volume means increased resource availability (Basset et al. 2003) and therefore a richer herbivore community (e.g. Basset et al. 1999, Basset 2001a, Caraglio et al. 2001, Barrios 2003, Novotny et al. 2003), and respectively, an increased host offer for the parasitoid Hymenoptera.

During the wet seasons differences between the study sites are not significant (after post hoc test). During the first dry season parasitoid Hymenoptera are significantly more abundant in the Yala fragment (than at Busambuli River and on *Heinsenia* at Colobus Trail) and during the second dry season they are significantly more abundant at Busambuli River (than in the Yala fragment, at both collecting units at Colobus Trail and in Kisere Forest). In both cases also the total number of arthropods is largest at these sites. Since the abundance of parasitoid Hymenoptera is highly significantly correlated with all other taxa collected ($p < 0.001$, except Formicidae), one can assume that a host-parasite correlation exists and their large numbers can be explained more likely with an increased food supply, instead of fragmented or disturbed habitats. Due to the enormous species richness of the parasitoid Hymenoptera (e.g. Noyes 1989, Askew 1990, Stork 1991, Horstmann et al. 1999), the species composition in the assemblages is unknown and further statements, whether they are host specific or generalists, cannot be made, especially since correlations of parasite-host relationships as well as their auto-ecology and synecology are only rarely studied or unknown (Memmot et al. 1993, Godfray et al. 1999).

Homoptera

Homoptera are represented with a proportion of 10.89 % (N = 26,560, Fig. 9, p. 31). Within this group Aphidoidea and Cicadoidea are the most dominant taxa. The differences between study sites are significant; during the first wet season Homoptera were most abundant at the Yala site ($p < 0.01$), while during the second wet season most individuals were found at Busambuli River ($p < 0.001$). During the dry seasons, Homoptera were most abundant in the Kisere Forest ($p < 0.05$ for I.2002; n.s. for I.2003) and this is similar to the distribution pattern of ants in this fragment, maybe due to mutualistic correlations of both groups, respectively a particular ant species in that part of the forest. Also differences between wet and dry seasons are highly significant ($p < 0.01$) with increased numbers of individuals during the wet seasons. Similar results are presented by Wolda (1979) and Novotny & Basset (1998), where sap-sucking insects in the canopy of tropical rain forests reached their maximal abundances also during the wet season. Again, this can be explained by accumulating along a gradient of humidity. Aphids are certainly very abundant in the tropics, but they are thought to be quite poor in species (Price 1991), since most of them are very host specific, but due to ineffective mechanisms of host finding, they are probably not able to find or effectively use their rare and randomly distributed host plants in the very rich vegetation of tropical forests (Dixon et al. 1987).

There are some other taxa, where seasonality has a strong influence on their abundance and distribution, respectively. It seems that larvae of Symphyta are mostly restricted to humidity, since they occur during the wet season only ($p < 0.001$), with only a very few exceptions. Adult Symphyta were extremely rare in all assemblages, because as good flyers they were also able to escape the fog. Within the wet seasons the larvae are only present (and significantly more abundant) along Isiukhu River and Busambuli River, in the first wet season also in the Kisere Forest. The close distance of these sites to a river and accordingly the resulting wet environment is obviously essential for the development of the larvae. Since these larvae are exclusively phytophagous, the leaf-flush period is probably also of importance to the alternation of generations. Both facts are correlated with the beginning of the wet season (Basset 1992b, 1996), where an increase of plant growth provides new food resources (Denlinger 1986). Young leaves are supposed to be more nutritional (Coley & Barone 1996), since defence ingredients like fibre, lignin, silica, tannins, oils, waxes and resins, which reduce the digestibility of leaves, increase with the leaf age (Scriber & Slansky 1981). Old leaves are also three times harder than new ones (Jolivet & Hawkeswood 1995). This is correlated with the already known phenomenon of phytophagous insects preferring younger instead of older, more sclerotised leaves (Cates 1980, Aide & Zimmerman 1990, Bach 1990, Coley & Aide 1991, Jolivet & Hawkeswood 1995).

These facts generally apply to all phytophagous insect groups, which feed on leaves, such as caterpillars and some Ensifera, which are also more abundant during wet seasons ($p < 0.05$ for caterpillars, $p < 0.001$ for Ensifera), but of the latter group generally few individuals could be found. Some plant species have evolved to avoid the impact of feeding by starting their leaf-flush before the usual beginning of the wet season or by producing very fast and synchronously large amounts of leaves and that way an excessive supply for phytophagous insects (Aide 1992, 1993). Reasons, why caterpillars could be more regularly found on *Heinsenia* than other phytophagous insects, might be either due to poor adaptations to the secondary ingredients of the leaves of *Teclea* or higher specialisation to the leaves of *Heinsenia*. Since the leaves of *Teclea* have a somewhat tougher consistence and contain defences against herbivory such as ethereal oils, which are typical for Rutaceae, the first assumption is more likely.

Similar to caterpillars and tree crickets are the distribution patterns of Acari, since the impact of seasonality on mites is also very strong ($p < 0.001$). This group is most abundant along the Isiukhu River and the density of moss growth on tree trunks should provide enough humidity and cover against predators during the dry season. The increased humidity in this area due to the close distance to the river might also explain the high abundance at Busambuli River during the second dry season, but this scenario

is not useful in explaining the large numbers of mites at Colobus Trail during the first wet season.

4.2. Distribution patterns and seasonality of beetles

In contrast to the results of the arthropods, the assemblages of beetles at the different study sites show a clearer pattern. The numbers of beetles collected at Isiukhu River, on *Heinsenia* at Colobus Trail and in Kisere Forest are quite similar in all seasons and differences in the abundance of beetles between wet and dry seasons are not remarkable and not significant (Fig. 18, p. 45). At least for the site along the Isiukhu River one could suggest that constant conditions of humidity are present due to the very close distance to the river. These conditions probably do not vary to a large extent between dry and wet seasons and the beetle communities are well adapted to this environment and are able to maintain populations of the same size during the dry season. However, this explanation does not fit at all for the two other sites, since there are no rivers in the vicinity of the sites and differences of humidity between wet and dry season were more pronounced than along the Isiukhu River. There are obviously other mechanisms responsible for regulating the population densities of beetles at these sites, but this will be discussed later. At Busambuli River, on *Teclea* at Colobus Trail and in the Yala fragment generally more beetles could be found during wet seasons than during dry seasons (with only one exception, namely at Busambuli River in the second dry season, where the highest number of beetles per season is recorded). This trend certainly applies for all beetles collected, since the mean number of individuals during wet seasons is significantly higher than during dry seasons ($p < 0.05$), but obviously seasonality does not influence the abundance of all beetle taxa in the same way. Since comparisons of all taxa between sites and seasons show no distinct patterns, general predictions about beetle abundances based only on seasonality and accordingly on rainfall and humidity are not possible. Due to the different biology and life cycles of each feeding guild and the resulting susceptibility to seasonality, each of the guilds investigated will be discussed in detail.

Predacious beetles
Focussing on the feeding guilds investigated, only the individuals and species numbers of predacious beetles are significantly higher during both wet seasons than during both dry seasons ($p < 0.001$ for species, $p < 0.05$ for individuals). The high influence of seasonality is also clearly shown by the Cluster and Correspondence analyses (Fig. 21, Fig. 22, p. 51). This might be due to a predator-prey relationship and that most of the adult carnivorous beetles feed on insects and their larvae which are more abundant

during wet seasons, especially since ants do not have a considerable influence as top-predators on the arthropod communities, as discussed before. Some predators are probably specialised to drought or on prey that is more abundant during the dry season (e.g. psocids). Besides lower species numbers, also lower evenness and larger faunal overlap between the study sites during the dry seasons are a point in this favour, indicating that only few, but generally the same species are dominant in the dry season (Table 7, Fig. 23, pp. 49, 53). This could be perhaps a strategy of avoidance of interspecific competition, but this is rather unlikely for this feeding guild, since in wet seasons prey as food resource should not be limited in the tropics and therefore, a general adaptation on different climatic conditions is more likely. Regarding the accumulation curves of all four feeding guilds investigated, it is shown that the proportion of "new", not yet collected species is very high for predacious beetles (Fig. 19, p. 47). Due to the high proportion of singletons in the samples, the curve does not reach a plateau or saturation point even after the fourth sampling event, indicating that much more samples will be necessary to collect the entire fauna of predacious beetles in this forest (see also Table 11, p. 82).

Mycetophagous beetles

Contrary to predacious beetles, the fauna of mycetophagous beetles has been more completely recorded even during the first sampling session and after that, new species could only be found irregularly from time to time (Fig. 19, p. 47). The proportion of species found only once in the samples is also comparably low (Table 11, p. 82). However, the allocation to morpho-types for instance of Corylophidae has been somewhat difficult, since all specimens are more or less of the same habitus, size and even colouration and thus, very hard to distinguish. Therefore, under estimation of species numbers is quite likely, especially since time-consuming genital-dissections were not performed on the several thousand beetles sampled.

The analyses for the mycetophagous beetles do not show significant differences between the sites nor between the seasons, although on average more species could be found during the wet seasons. Single species are very dominant which can be also derived from high faunal overlap between sites and seasons (Table 8, Fig. 27, pp. 55, 59), but there is no indication that seasonality is of great importance for fungivore beetles. The food supply is obviously quite constant at the study sites throughout the year. Only on *Teclea* and *Heinsenia* at Colobus Trail the impact of seasonality is apparently recognisable, since more species and individuals could be found during both wet seasons. The availability of fungi is perhaps reduced during the drought, which is probably more severe and pronounced at this site, because of its small size and the lack of streams in the vicinity of the trees investigated.

Leaf beetles

For leaf beetles, certainly more species could be found during wet seasons (but without significant differences), but in comparison to the dry season significantly fewer individuals ($p < 0.001$). As mentioned before, phytophagous beetles might be highly influenced by seasonality, since wet seasons provide new food resources for phytophagous insects in general (Denlinger 1986), due to the higher nutritional quality of young leaves (Coley & Barone 1996) and the usually lower concentration of secondary plant products in young leaves (Scriber & Slansky 1981). Dependency on young leaves has already been observed for leaf beetles; the Colorado potato beetle (Chrysomelinae) for instance, when feeding on senescent leaves usually stop its reproduction and can be rapidly forced into diapause (de Wilde 1969) and larvae of *Paropsis* (Chrysomelinae) only prefer new leaves, otherwise their normal development is disturbed (Larson & Ohmart 1988). Also the leaf geometry seems to affect the food selection by phytophagous insects, since e.g. leaf rollers and leaf chewers each prefer different leaf aspects of the same tea cultivars (Banerjee 1987). But the supply of food is probably more important for the larvae of phytophagous beetles and hence, they hatch at the beginning of the rainy seasons. Maybe mating, copulation and reproduction cycles occur in the dry times and therefore more adult beetles could be found then, when conditions are unfavourable for the larvae. In the dry season with decreasing food resources, species may survive as eggs, pupae or even adult beetles, which are not as dependent on young leaves. Wagner (2003) found also increased abundances of phytophagous beetles (Curculionidae, Apionidae and Alticinae) during the dry season in a rain forest in Uganda. However, seasonality does not influence this group to the same extent as predacious beetles.

Faunal overlap and dominance of leaf beetles are on average higher in the dry seasons, but faunal composition is most similar within both collecting units of *Heinsenia* and also the dominance of single species is only clearly increased on this tree species at Colobus Trail and in Kisere Forest (Fig. 31, Table 9, pp. 65, 61). These values indicate a higher influence of host specificity than of seasonality; this is also clearly shown in the Correspondence and Cluster analyses (Fig. 29, Fig. 30, p. 63), but this fact will be discussed later in a separate section. Neither species numbers nor faunal overlap is affected by decreasing habitat size, but faunal overlap is strongly decreasing with increasing distances between the sites investigated ($p < 0.05$ for wet season, $p < 0.001$ for dry seasons), showing that the species composition might be also influenced by different forest types. But one should take into consideration that these results are most likely distorted by the proportion of host specific species, since *Heinsenia* was investigated only in the northernmost study sites, while in the southern part of the forest only *Teclea* was investigated. The assemblages of leaf beetles also consist of many

singletons (Table 11, p. 82) and therefore, probably only a small proportion of the complete leaf beetle fauna in this area has been collected.

Weevils

The same assumption applies for weevils, since they have the highest proportion of singletons of all feeding guilds investigated (Fig. 11, p. 32). Weevils and leaf beetles constitute the most diverse and abundant feeding guild of the entire beetle fauna. The total number of species is lower as for leaf beetles, but generally more individuals per tree could be found (Fig. 19, p. 47). The evenness is on average lower as in the other guilds investigated and despite the high amount of singletons, some species are very dominant and attain comparably high population densities. However, the diversity structures of weevils at the study sites are quite similar and no significant differences between seasons or study sites could be found at all, although on average more species could be found during the wet seasons (Fig. 32, p. 68). An explanation of these results is probably similar to those discussed for leaf beetles and seasonality influences the diversity structure of weevils only to a small extent. Cluster and Correspondence analyses show again an influence of host specificity, but also influence of forest type seems to be important for weevils, shown by the strict clusters for all samples of Busambuli River, the Yala fragment and to a lower extent of *Heinsenia* at Colobus Trail (Fig. 33, Fig. 34, p. 69). The faunal overlap within the study sites is generally very high, especially within both collecting units at Colobus Trail, indicating correlation of the faunal composition of weevils and distance of study sites. Actually, faunal overlap decreases significantly with increasing distances between the study sites ($p < 0.01$ for wet seasons, but n.s. for dry seasons). This pattern can be explained by the high proportion of flightless Curculionidae, which cannot move rapidly or travel long distances between the study sites. Rivers, open grassland and maybe even roads might act as boundaries for the dispersal of these species and therefore, they are restricted to a smaller area than beetles that are capable of flight. For this reason, it is also conceivable that these beetles are rather generalists than specialists, due to difficulties in finding single host plants which show a very scattered distribution in tropical forests (Basset 1992a). Therefore, it is more likely that they are influenced by forest type and habitat structure than by the presence of possible host plants, although no significant differences between the sites are recognisable. Neither species numbers nor faunal overlap show significant differences with decreasing habitat size.

4.3. Critical considerations on the methodology

The high proportion of rare species in assemblages of tropical arthropods causes difficulties in investigating species diversity, composition and turnover (Table 11). The question of McArdle (1990), when is a rare species really rare or just not there, can only be answered by an exhaustive search of the entire habitat, which is certainly not possible in a tropical rain forest. On this condition the real local abundance of rare species is quite unknown and cannot be reliably estimated with extrapolating methods (Colwell & Coddington 1994).

Table 11: Overview of singletons found during all four sampling events; S_{total} = total number of species, (n) = number of singletons, (%) = percentages of singletons.

	predacious beetles	mycetophagous beetles	Chrysomelidae	Weevils	Coleoptera (others)	Coleoptera (total)
S_{total}	179	54	134	124	532	1023
Singletons (n)	70	14	42	55	259	440
Singletons (%)	*39,1*	*25,9*	*31,3*	*44,4*	*48,7*	*43,1*

Depending on the richness estimator used, i.e. how much the proportion of singletons is weighted in the calculation, enormous variations in the estimated species numbers were calculated in this study. This way, e.g. between 65 and 134 species of predacious beetles have been estimated for the collecting unit of *Heinsenia* at Colobus Trail (Table 7, p. 49; X.2002), based on 36 species collected of which were 19 singletons (= 53 %). That means from about two times to nearly four times more species than actually observed are expected for this site and these more unlikely values should emphasize the difficulties of extrapolating methods. Therefore, the rarefaction method, which is based on intrapolating species numbers, was more reliable for the assessment and comparison of species richness.

Generally, this work was conducted with a standardised sampling regime. In detail, the concentration of insecticide used and duration of fogging was similar and also the area of sampling sheets amounted to 16 m² was constant for each fogging event. However, this method is strongly dependent on weather conditions. Many small insects are probably affected by the washed out effect after heavy rains (New et al. 1991). Fogging after these rains might not be as successful, but this would be a general problem also for other sampling regimes. Sometimes the usual drop time of 90 minutes could not be kept up, due to sudden weather changes after fogging and this led to a reduced drop time of only 45 minutes. To what extent the total number of arthropods collected was influenced by these incidents is hard to estimate.

Despite this standardised method the numbers of beetles collected are strongly variable for each tree. On the one hand the distribution of these animals in time and space is driven by chance effects (Kareiva 1990, Williamson & Lawton 1991), but on the other hand the canopy volume and number of individuals are positively correlated. Generally, trees of the same height should be chosen, but in the tropics it is hard to find enough adequate trees and therefore, the heights of the trees investigated ranged from six to twelve meters for *Teclea nobilis* and five to nine meters for *Heinsenia diervilleoides*. Differences in the canopy volume are accordingly higher, especially since the density of branches and leaves is also subject to variation. But the effects of individual differences should have been minimized, since a unit of eight trees per site has been investigated.

Another possible factor that might result in strong differences in abundances of arthropods collected is the fact that the same trees have been refogged three times. One could expect fewer arthropods during both dry seasons, since there was an interval of only three months between wet seasons and dry seasons, while more than seven months passed between dry seasons and wet seasons. But the numbers of arthropods of the last fogging events in October 2002 and January 2003 are larger than the first ones in October 2001 and January 2002. In addition some studies on recolonisation of arboreal arthropods (Erwin 1989, Stork 1991, Stork & Hammond 1997), show that faunal recovery happens quite rapidly and thus, three months should be enough time for arthropods to recolonise the trees after fogging.

As mentioned before, phloem-feeders, gall-builders, leaf-miners and internal feeders such as wood borers are only collected by chance (Stork & Hammond 1997). Despite these disadvantages, there is no comparable method which allows a quantitative sampling in such an efficient manner (Basset et al. 1997), since other canopy dwelling arthropods, which live on the surface of leaves and twigs, can be nearly completely collected with the fogging method. For instance colour traps or flight-interception traps only attract or trap flying insects and represent their activities, but not their true abundance. Moreover, they only capture a fraction, and this is usually an unknown fraction of the resident fauna and insects cannot be reasonably allocated to a certain host plant (De Dijn 2003).

4.4. Herbivory, host plant specificity and global diversity

The high diversity of phytophagous insects is generally explained by the high degree of specialisation on host plants. Driven by the co-evolution of plants and phytophagous insects even since the early Tertiary, plants have developed continuously new chemical

and mechanical defences against damage caused by pests. Due to better protection by a novel antiherbivore defence (e.g. latex and resin canals), these plants were probably temporarily freed from herbivore pressure and could grow more freely and frequently and finally, become more diverse than plants without protection mechanisms (Farrell et al. 1991). As mechanisms of avoidance and detoxification evolved again by any herbivore user, it could feed exclusively on this resource and now diversify for its part, too (Farrell et al. 1992, Jermy 1994). Due to these mutual adaptations, even intraspecific differences by genetic variation of parts of plants can decide the utilization of phytophagous insects (Price et al. 1980, Fritz & Price 1988) and it is suggested that the higher diversity and chemical defences of plants caused by these intense interactions leads to higher specialised insects (Godfray et al. 1999).

Mimicry can also function as a potential anti-herbivory adaptation; e.g. extra-floral nectarines of *Passiflora* vines mimicking butterfly eggs and therefore repelling females of Heliconiinae to lay their eggs on the apparently "occupied" plant (Jolivet & Hawkeswood 1995) and the irregular shape of some Moraceae plants seems to mimic feeding-damage and earlier colonisation by herbivores (Niemelae & Tuomi 1987), assuming that visually-searching herbivores avoid host plants which have been colonised earlier. This has not been explicitly recorded for leaf beetles, but it is known that beetles, butterflies, moths and other herbivore taxa exclude each other for instance on young *Cecropia* trees (Jolivet & Hawkeswood 1995).

Since the ecology of most afrotropical herbivores is still insufficiently studied and life cycles, feeding behaviour and host plant relationships are poorly described, it is still not known if host plant specificity is really a common phenomenon within tropical phytophagous insects (Novotny et al. 2002b). The resource fragmentation hypothesis denies this assumption and supposes that higher diversity of plants leads to lower population densities, thus to lower host specificity (Godfray et al. 1999). However, studies on Palaearctic and Nearctic leaf beetles prove the dominance of host specialists in the temperate zones (Koch 1992), e.g. one of these studies shows that 298 species of leaf beetles in North America feed on average on only 1.5 host plants (Strauss 1988) and in Central Europe about 80 % of Chrysomelidae are mono- or oligophagous (Schöller 1996). This is certainly not the case for the tropics; there are some highly specialised phytophagous insects such as Heliconiinae on Passifloraceae (Benson 1978) or Bruchinae and other beetles which feed on seeds of Fabaceae and Caesalpiniaceae (Janzen 1980), but there is very little known about canopy dwelling leaf-eating insects and some works show a rather low host specificity for herbivorous insects (e.g. Novotny et al. 2002b, Ødegard 2003).

What might be the causes of low host specificity in the tropics? Many bark-beetles, leaf beetles and weevils evolved excellent capabilities and strategies for finding their hosts even over long distances. But due to the considerable random distribution and rarity of many plants in tropical forests, the search behaviour might become too drawn out and ineffective (Basset 1992a). Loss of energy and time cannot be compensated by the advantages of specific adaptations such as better nutritional utilization of secondary ingredients in the plants. Also the low air circulation in tropical forests is certainly of importance, since some of these beetles are known to move along a wind-induced concentration gradient.

By calculating the degree of specialisation of beetles, the question arises, when is a species confidently and effectively specialised on a host plant? Should the large number of species found only once (i.e. the proportion of singletons) and therefore, imperatively associated on only one tree species, be regarded as host specific and, if not, from which number of individuals would this be the case? Table 12 shows the proportion of species exclusively found either on *Teclea nobilis* or *Heinsenia diervilleoides* for different conditions, that means based on different numbers of individuals. For example in column "≥ 10" only those species are included, which are represented by a minimum of ten individuals, whereas in column "≥ 1" even singletons are included.

Table 12: Host specificity of beetles for different conditions; $S_{exclusive}$= number of species exclusively found on only one tree species, $N_{ind/spec}$= number of individuals per $S_{exclusive}$ (e.g. in column "≥ 10" only those species are included, which are represented by a minimum of ten individuals, in column "≥ 1" even singletons are included).

taxon (number of species)	≥ 1	≥ 2	≥ 5	≥ 10	$N_{ind/spec}$
Chrysomelidae (134)	87	45	22	14	$S_{exclusive}$
	64,9	*33,6*	*16,4*	*10,4*	*host specificity (%)*
Weevils (124)	94	39	10	7	$S_{exclusive}$
	75,8	*31,5*	*8,1*	*5,7*	*host specificity (%)*
mycetoph. beetles (54)	22	8	2	1	$S_{exclusive}$
	40,7	*14,8*	*3,7*	*1,9*	*host specificity (%)*
predacious beetles (179)	109	39	14	7	$S_{exclusive}$
	60,9	*21,8*	*7,8*	*3,9*	*host specificity (%)*
Coleoptera (others) (532)	395	136	44	17	$S_{exclusive}$
	74,3	*25,6*	*8,3*	*3,2*	*host specificity (%)*
Coleoptera (total) (1023)	708	268	93	46	$S_{exclusive}$
	69,2	*26,2*	*9,1*	*4,5*	*host specificity (%)*

This overview illustrates the fact of decreasing host specificity dependent on the definition of how many individuals of one species are necessary to "define" it as an effective specialist. The proportions in the first column are certainly not useful for comparisons, beside the fact that the real proportion of specialists within the large number of singletons (see also Table 11) remains absolutely unknown. After the examination of all 192 trees (124 trees of *Teclea nobilis* and 64 trees of *Heinsenia diervilleoides*), it is concluded that an individual number of more than ten per species exclusively found on one tree species should be evidence of host specificity and the effects of chance are quite unlikely. This proposal is supported by the fact that most of those exclusive species are represented by far more than 100 specimens and could be found at all sites studied.

What does this mean for diversity in a global frame? Erwin (1982) argued in his famous estimation of global diversity as followed: beetles represent roughly 40 % of all known arthropod species and the canopy fauna is at least twice as rich as the forest floor fauna. Citing an estimate of 50,000 species of tropical trees, Erwin thus estimated 30 million tropical arthropods in total, based on 162 host specific species of beetles per tree species collected on 19 trees of *Luehea seemannii* in a rain forest in Panama. Using Erwin's calculation and the present results based on 46 host specific species (represented by more than ten individuals) for a lower estimate and assuming 93 host specific species (represented by more than five individuals, see Table 12) for the upper range, one would estimate between 4.3 and 8.7 million species of tropical arthropods. Since two tree species are involved in this calculation, one should note that the number of tropical trees has been bisected in the equation. This number is attributed to a clearly reduced proportion of specialist from 13.5 % in Erwin's estimation to 4.5 and 9.1 %, respectively in this work (Table 12, Coleoptera total). A lower proportion of host specificity is also confirmed in many studies which referred to Erwin (May 1986, 1990, Thomas 1990, Gaston 1991b, Hodkinson & Casson 1991, Basset 1992a, Hodkinson 1992, Hammond 1994, Simon 1996, Mawdsley & Stork 1997, Novotny et al. 2002b). Ødegard (2003) found a similar degree of specialisation (7−10 %) in his studies on taxonomic composition and host specificity in a dry forest in Panama. The study was carried out from a gondola connected to a tower crane by observing and counting host visits of phytophagous beetles on a total of 50 plant species (26 liana species and 24 tree species).

In conclusion, the proportion of host specialists is clearly lower than predicted and ranges from about 2−4 % for fungivore beetles to about 10−16 % for leaf beetles; 4−9 % host specificity is calculated for Coleoptera in total. Such comparisons and calculations always contain some errors, because it is not known, if adults or larvae of

phytophagous beetles really feed on *Teclea nobilis* (Rutaceae) or on *Heinsenia diervilleoides* (Rubiaceae). Or whether they are mono-, oligo- or polyphagous, since experiments on species ecology or knowledge about feeding behaviour and plant-insect relations are not available. Rutaceae are aromatic plants and have complex secondary compounds, most of them are from the genus *Citrus* and many of them are xerophytic. There are two types of leaf beetles frequenting Rutaceae, the mono- or oligophagous species and the polyphagous species, which appear sporadically on the plants where they eventually nibble the leaves, but these plants are not the real hosts (Jolivet & Hawkeswood 1995). It is already known that the *Citrus*-feeding Chrysomelidae are not all restricted to Rutaceae (Jolivet 1979). Some of these beetles, like some Cassidinae and Alticinae use the young leaves only as secondary food resources in response to sudden climatic changes (Jolivet & Hawkeswood 1995).

Most of the chrysomelids known from Rubiaceae such as some species of Eumolpinae, Cryptocephalinae and Alticinae are generalists, and although it is one of the largest families of plants, surprisingly few Chrysomelidae feed on leaves of Rubiaceae, e.g. *Timarcha* (Chrysomelinae), *Sermylassa* (Alticinae) and *Neolochmaea* (Galerucinae). Differences in the feeding behaviour can even be noticed within subfamily level of Chrysomelidae. But why Cassidinae, Hispinae, Criocerinae, Chrysomelinae, Megalopodinae and Alticinae are mostly represented by mono- or oligophagous species, while others contain mostly polyphagous species, e.g. Galerucinae, Donaciinae, Clytrinae, Cryptocephalinae and Eumolpinae, remains unresolved. Due to the fact that the various plant families on which they feed differ considerably in their chemical composition, they must have a common attractant or at least a lack of repulsive substances. In this context the reaction of plants on feeding damage with synthesis of repellent substances should be mentioned, which also affect other phytophagous insects. Also the production of allomones by the plants, which attract predators and parasitoids of herbivore insects is of importance (Price et al. 1980).

However, the most specious phytophagous insects are leaf beetles and weevils. One possibility why leaf beetles and weevils could be present in the canopy of *Teclea nobilis* and *Heinsenia diervilleoides*, but do not feed on the leaves, can be explained at least for the assemblages during the dry seasons. During the dry periods many herbs dried up, and perhaps some of the beetles chose these trees as resting sites along a gradient of humidity and the canopies represent relatively moist places (Wagner 2001). Aggregation and sometimes even diapause of beetles during dry seasons in the tropics at such places have been reported, for example, in Coccinelidae (Wolda & Denlinger 1984), Galerucinae (Masaki 1980) and Cassidinae (Flowers 1991). Nevertheless, it is not absolutely necessary to feed on a plant to be a specialist: host specificity means for

phytophagous beetles that they must use this tree species in some way for successful reproduction, predators are tied to one or more of the herbivore species, scavengers are associated in some way with only the tree or with the other trophic groups and mycetophagous beetles are tied to fungi associated only with this tree species (Erwin 1982).

As also shown by the faunal overlap of leaf beetles and weevils (Fig. 31, Fig. 35, pp. 65, 71) and by the multivariate analyses (Fig. 29, Fig. 33, pp. 63, 69), Curculionoidea have a lower degree of specialisation than Chrysomelidae, namely about six to eight per cent, compared with ten to 16 per cent within the leaf beetles. The faunal overlap within one tree species compared to the overlap between both tree species is also significantly higher for Chrysomelidae than for Curculionoidea (Chrysomelidae: $p < 0.001$ for both seasons, Curculionoidea: $p < 0.01$ for wet seasons, n.s. for dry season). As mentioned before, this might also be due to the proportion of flightless weevils and the resulting difficulties in host location, because of decreasing densities of host plants in tropical wet forests (Janzen 1970, Basset 1992a). It is not absolutely necessary to find a suited host, since some phytophagous insects never leave their host plant during their whole lifetime, but this would be at least from time to time important for the dispersal and distribution of the population and species, respectively. Nevertheless, many studies show that host specificity of leaf beetles and weevils in tropical regions is lower than in temperate regions (e.g. Strauss 1988, Koch 1992, Schöller 1996, Mawdsley & Stork 1997, Novotny et al. 2002b, Ødegard 2003). This might be a common phenomenon in the tropics, since unpredictability and rarity of resources lead to a larger niche of species and finally to a higher degree of polyphagy (Futuyma 1976, Jermy 1985, Michaud 1990). This is also known from successional stages in temperate regions, e.g. where the proportion of generalists within the weevils is positively correlated with the increase of plant diversity during succession (Brown & Hyman 1986).

Any change in tree species composition caused by logging or fragmentation of tropical forests will have a major impact on temporal variation in resource availability, and hence on arthropod assemblage dynamics (Didham & Springate 2003). Species which are associated with only one host plant, no matter to which trophic guild they belong, have one great disadvantage in common: if they are not able to shift to another host plant, selective logging of their host trees would be a threat on these species and might even be the reason for their extinction, at least of some populations. To avoid this problem, a drastic food change in response to the loss of their host plant is required. This behaviour is known as allotrophy and often occurs under stress conditions (Jolivet & Hawkeswood 1995), but it has not really been well analysed (Jolivet 1986). Allotrophy must not be confused with polyphagy, moreover it is a survival strategy, e.g. for the

Alticinae which feed on *Quercus* (Fagaceae) in Europe and on *Carica* (Caricaceae) and *Psidium* (Myrtaceae) in the tropics where the normal food plant is absent; several other cases of allotrophy are known among the Chrysomelidae and sometimes the change in food plant preferences might result in the formation of new races (Jolivet & Hawkeswood 1995). On the other hand, the increase in numbers of taxonomically related host plants in tropical forests would favour host switches of herbivores (Novotny et al. 1999, Novotny et al. 2002a, Novotny et al. 2003).

4.5. Does fragmentation of forests influence beetle communities?

Once again: fragmentation, by definition, results in a reduction in habitat area and a concomitant decrease of living space for plants and animals, with almost inevitable reduction in species richness in remaining habitat fragments (Diamond 1972, Didham 1997b). Thus, habitat fragmentation is a major cause of biodiversity loss in tropical and temperate forests (Saunders et al. 1991, Tabarelli et al. 1999), and besides species diversity also abundances are affected, since population densities of species are also reduced in smaller habitats (Turner 1996, Debinski & Holt 2000, Laurance et al. 2002). According to the theory of island biogeography (MacArthur & Wilson 1967), population densities in fragments are dependent on the colonisation rate of new individuals as well as on the likelihood of stochastic population extinctions. As studied by Didham et al. (1998a) common species were significantly more likely to become locally extinct in small fragments than rarer species. This supports the model of multispecies coexistence under disturbance which suggests that competitively dominant but poorly dispersing species are the first to become extinct from habitat destruction (Didham et al. 1998a). Thus, rarer species are predicted to be better dispersers and better at persisting (Didham et al. 1998a). This fact would lead to an increasing proportion of rare species and decreasing faunal overlap in small fragments. Generally, faunal overlap is most obvious between different habitat types (beta diversity) and over large distances, or across dispersal barriers, within the same habitat (gamma diversity) (Cody 1993).

But responses to forest fragmentation are varied and contrasting: e.g. some butterfly assemblages show a significant decrease in species richness in small forest fragments (Shreeve & Mason 1980, Thomas et al. 1992, Rodrigues et al. 1993, Daily & Ehrlich 1995), whereas others show the reverse trend due to invasion of species from outside the fragments (Bierregaard et al. 1992, Brown & Hutchings 1997). Ozanne et al. (1997) investigated canopy arthropod communities in coniferous forests in southern Britain, with edge assemblages differing from that deeper in the forest and overall abundance

dropped significantly near the edge, with small organisms (Coleoptera included) being particularly affected. Helle and Muona (1985) found elevated abundance at forest edges in several beetle taxa and whole communities in the forest core have been identified as differing in composition from those near the edges (Halffter et al. 1992, Buse & Good 1993, Halme & Niemalä 1993). Didham et al. (1998a) found in their study that beetle species composition was more variable among edge sites than among undisturbed forest sites; thus, fragmentation appeared to increase beta diversity. Malcolm (1997) found in his studies an increase in understorey and a decrease in overstorey arthropod biomasses along primary forest edges which could be predicted from measurements of forest structure and appeared to be independent of any island effects. And while Ås (1993) did not find any species area effect operating on beetle diversity in large (> 120 ha) and small (< 20 ha) patches of deciduous forest, Martins (1989) showed that the abundance and species richness of *Drosophila* increased in small (one and 10 ha) forest fragments due to an influx of disturbed habitat species.

Forest core area versus forest edges

An increase of insect abundance and diversity at the forest edge is almost certainly due to the invasion of generalist species from disturbed habitats outside the forest fragment (Didham 1997b). Many of these species may be tree-fall gap specialists and can be extremely common at edges (Didham 1997b), whereas the response of small organisms, which decline in proportion at the edge, suggests that the dense forest structure provides more favourable conditions for many invertebrates than the exposed edge (Ozanne et al. 1997). Forest fragments are complex habitat islands (Didham 1997b) which are themselves modified to a large extent by the proximity of adjacent secondary habitats (Lovejoy et al. 1984, Lovejoy et al. 1986, Kapos 1989, Malcolm 1994, Camargo & Kapos 1995, Malcolm 1997). The penetration of external landscape influences into these habitats (Murcia 1995, Pickett & Cadenasso 1995) include hotter, drier and windier conditions at the edge than the forest interior, with a higher light intensity and modified plant composition and habitat structure (Kapos 1989, Williams-Linera 1990b, a, Malcolm 1994, Young & Mitchell 1994, Camargo & Kapos 1995, Kapos et al. 1997).

Generally, habitat fragments can be differentiated in two sub-habitats, namely the inner core area of a forest and the edge of a forest, including an edge penetration area (Laurance 1991, Laurance & Yensen 1991). This subdivision can be justified, because both sub-habitats clearly differ by biotic as well as abiotic factors (Murcia 1995, Laurance et al. 2002). Studies of Young and Mitchell (1994) indicate that edge effects may penetrate up to 50 m into forest stands, perhaps with a more severely affected zone within the first 15 m. Thus, insect communities in fragments are also influenced by

edge-induced habitat changes and their densities may vary, quite independently from insularisation (Murcia 1995), since the proportion of edge habitat is increasing with decreasing fragment size. However, edge specialists will also appear to prefer small fragments and edge avoiders to prefer large fragments (Didham et al. 1998a). The hypothesis of patch size effect is, that by a supposed constant population density within a sub-habitat, the population density of edge-specialists is increasing in smaller fragments, while the population density of core-specialists is decreasing (Bender et al. 2003). A beetle fauna characterised by a high number and random distribution of species, together with very low population levels, is typical of non-interactive communities with a high beta-diversity (Schoener 1986, Cornell & Lawton 1992). The biotope is not saturated with species, i.e. there are numerous vacant licences which can be used by randomly immigrating species, or these may be repeatedly vacated as a result of the extinction of small local populations (Kitching et al. 1997).

Edge effects would mostly affect the forest patches at Colobus Trail, Isiukhu River and Kisere Forest, because they are the smallest habitat areas investigated (see Table 13). All three sites are surrounded by open grassland or even plantations and random distribution of species is characterised by low faunal overlap, particularly along the Isiukhu River. However, the collecting unit investigated in Kisere Forest was much farther away from the forest edge than the trees at Colobus Trail and Isiukhu River.

Table 13: The study sites: isolation age, size, altitude (meter above sea level), distance of fragments to the main forest and distance of study sites to the forest edge; a.s.h. = adjacent secondary habitat (data partly from Brooks et al. 1999 and BIOTA E02 Landsat 7 (ETM+)-Scene 2001).

Study site		Isolation from main forest (years)	Size (ha)	Altitude (m a.s.l.)	Distance to main forest (km)	Distance to forest edge (type of a.s.h.)
Busumbuli River	main forest	-	8245	1600	-	inner forest
Colobus Trail	main forest	advanced	~200	1600	small corridor	low (road/grasland)
Isiukhu River	main forest	advanced	~600	1600	small corridor	low (river/grasland)
Kisere Forest	fragment	> 70	420	1500	1.6	high (plantation)
Yala River	fragment	> 30	1180	1400	4.1	high (plantation)

Predacious beetles

The study of Didham et al. (Didham et al. 1998a) indicates that edge-specialist species were predominantly predators, while edge-avoiding species were predominantly fungivores or saprophages; predacious species were more affected by forest fragmentation than species in lower trophic levels (Didham et al. 1998b). Extensive habitat and resource changes along edges will likely have important consequences for insect predators and for ecosystem function, and will complicate attempts to apply island biogeography theory to the study of tropical forest fragments (Malcolm 1997).

The loss of insect predators or parasitoids in fragmented habitats can favour pest outbreaks, if phytophagous insects are released from natural control by their antagonists (Kareiva 1987, Lasalle & Gauld 1991, Kruess & Tscharntke 1994). In the present study, differences of abundance and diversity of predacious beetle species between the study sites, respectively forest types are quite distinct. At Busambuli River and in the Yala forest fragment predacious beetles are very abundant and faunal composition shows the highest similarities, but dominance of single species is much higher than at the other sites and low evenness indicates low alpha-diversity. This also applies for the Kisere fragment, but similarities of faunal composition is lower, probably due to much fewer individuals and species collected. Species numbers at a common random sample in the rarefaction curves are significantly lower for Busambuli River and both forest fragments than numbers at Colobus Trail and Isiukhu River during both wet (p < 0.05) and dry seasons (p < 0.001; Fig. 20, p. 50). The species composition at Colobus Trail and the Isiukhu River differs even within the sites and between each season. Therefore, the community composition is unpredictable and highly influenced by stochastic events, due to high beta-diversity, variability of alpha-diversity and rarefaction curves, unpredictable species appearance and disappearance, and the obvious lack of successional stages or climax equilibrium (see also Floren & Linsenmair 1997). That would mean that these sites are probably more disturbed due to decreasing dominance of single species, decreasing species turnover and increasing species diversity of predacious beetles (Didham et al. 1998a, Floren & Linsenmair 2003). An increased species diversity in disturbed habitats could be proved for predacious beetles since species richness of Staphylinidae (Buse & Good 1993) and Carabidae (Duelli et al. 1990) were found to be significantly higher at forest edges and therefore more frequently in smaller fragments. Regarding predacious beetles, the sites at Busambuli River, in the Yala fragment and in Kisere Forest are accordingly less disturbed, since faunal overlap of these beetles is generally higher within and also between these sites (during both dry seasons) and therefore species composition is more predictable at these sites. The beetle community is less affected by influx of forest edge species and therefore, species numbers are comparatively low.

Mycetophagous beetles

The abundance and diversity of mycetophagous beetles are not influenced by different forest types. These beetles are quite homogeneously distributed between fragments and main forest and therefore, one can assume that the food supply is probably not disturbed by fragmentation and degradation of habitats; diversity and species composition are on their part only influenced by the availability of fungi. Samples of this guild show saturation at a level of 54 species (Fig. 19, p. 47). This indicates the presence of an interactive community of beetles. The number of coexistent species is

limited, nearly all niches are occupied and some successful species have high population densities. There are strong interactions between species on the same trophic level which leads to narrow niches (Cornell & Lawton 1992). If there is really interspecific competition for the food resource of fungi cannot be proved, but the low species numbers and high population densities are at least evidence for it. On the other hand microclimatic conditions are probably more important for the aggregation of mycetophagous beetles: humidity leads to an increased offer of fungi, which again attract more beetles, which on their part certainly prefer the increased humidity conditions, due to their very small size.

Phytophagous beetles

Wagner (2000a) showed, that the distribution of phytophagous beetles in tropical forests also depends on the structure and composition of the vegetation and on the different forest type of the sites, respectively and is therefore also influenced by fragmentation and degradation (see also Davies et al. 1997). This possibly applies for the weevil and leaf beetle communities in Kakamega Forest, since faunal overlap within the study sites is significantly higher than faunal overlap between the sites (Curculionoidea: $p < 0.001$ for both seasons; Chrysomelidae: $p < 0.01$ for wet seasons, $p < 0.001$ for dry seasons), but this can be just an effect of increasing distance, since trees of a collecting unit stand closer to each other than they do between the study sites. But comparisons of assemblages of different study sites collected on several tree species are very difficult, because differences in the faunal composition are not only caused by changes of habitat structures, since some species of phytophagous beetles might be host specific for the studied tree species (at least 10−16 % for leaf beetles, 6−8 % for weevils; Table 12). As shown before, the influence of seasonality is also important, since species composition differs between wet and dry seasons (Fig. 28, p. 62). Therefore, comparisons between sites are only reliable, if the assemblages are collected in the same season and on the same tree species. One should remember that in Kisere Forest *Heinsenia diervilleoides* was investigated and at the other sites *Teclea nobilis*, while both tree species were involved in the investigations at Colobus Trail and results and possible interpretations might not vary only due to differences in the habitat structure and forest type.

Nonetheless, the proportion of species numbers exclusively found at only one of the study sites has been calculated and, similar to the evaluation of host specificity, only those results were regarded, where singletons are excluded (Table 14). Thus, the percentages of exclusive species found in the main forest range from 6.2 to 8.8 % for leaf beetles and 4.7 to 10.6 % for weevils. In the Kisere Forest no exclusive phytophagous species could be found at all and in the Yala Forest fragment no

exclusive leaf beetles and the lowest proportion of exclusive weevils (4.3 %) could be found.

Table 14: Numbers and percentages of species exclusively found at only one study site

taxon ↓	study site →	Busambuli	Isiukhu	Yala	Colobus	Kisere	Average percentages
leaf beetles	species total	65	68	62	69	43	-
	exclusive at site	13	16	7	14	8	-
	%	**20.0**	**23.5**	**11.3**	**20.3**	**18.6**	**18.7**
	singletons	9	10	7	9	8	**-**
	excl. without singl.	4	6	-	5	-	**-**
	% without singletons	**6.2**	**8.8**	**-**	**7.8**	**-**	**3.2**
weevils	species total	58	42	46	66	37	**-**
	exclusive at site	23	8	10	23	5	**-**
	%	**39.7**	**19.0**	**21.7**	**34.8**	**13.5**	**25.7**
	singletons	19	6	8	16	5	**-**
	excl. without singl.	4	2	2	7	-	**-**
	% without singletons	**6.9**	**4.7**	**4.3**	**10.6**	**-**	**5.3**
predacious beetles	species total	74	83	90	113	66	**-**
	exclusive at site	10	13	13	30	14	**-**
	%	**13.5**	**15.7**	**14.4**	**26.5**	**21.2**	**18.3**
	singletons	10	9	11	28	12	**-**
	excl. without singl.	-	4	2	2	2	**-**
	% without singletons	**-**	**4.8**	**2.2**	**1.8**	**3.0**	**2.4**
mycetophagous beetles	species total	34	33	35	34	28	**-**
	exclusive at site	3	4	7	5	1	**-**
	%	**8.8**	**12.1**	**20.0**	**14.7**	**3.6**	**11.8**
	singletons	1	3	5	4	1	**-**
	excl. without singl.	2	1	2	1	-	**-**
	% without singletons	**5.9**	**3.0**	**5.7**	**2.9**	**-**	**3.5**

These results show at least a trend that in both fragments less exclusive species occur. But the questions remains, if this is really caused by faunal relaxation (i.e. loss of forest dwelling species) or if the other sites are invaded by non-forest species and consist of forest edge specialists or even open grassland species. The higher proportion of exclusive species found at the other sites might be caused by the influx of a different beetle fauna, which is associated with different plant compositions of the adjacent secondary habitats. These species would not have been recorded within the fragments, because the trees investigated were situated quite far from the forest edge and therefore most likely out of range of the edge penetrating area (Young & Mitchell 1994). Wagner (2000a) found higher proportions of species exclusively found in a special forest type. He studied leaf beetle species in the Budongo Forest, Uganda, which are restricted to only one of three forest types investigated (i.e. primary, secondary and swamp forest) and calculated an arithmetic mean of 32.5 % including and 16.5 % excluding singletons, respectively. In the present work the arithmetic mean for exclusively found species is 18.7 % (4.6 % without singletons) for leaf beetles and 25.7 % (5.3 % without singletons) for weevils. By such low proportions of habitat-typical species, especially if singletons are excluded, it is doubtful, if the habitats within the

main forest and within fragments really differ to a similar degree as it was the case in Uganda, where four different tree species were investigated and the habitats investigated were much more distinct than in Kakamega Forest. This might be one reason why phytophagous beetles in Kakamega Forest do not seem to be greatly influenced by the structure of forest habitats.

If differences between study sites are not caused by different habitat types, maybe influence of edge effects might be the reason for different faunal composition. Didham (Didham 1997b) found both strong edge effects and strong area effects influencing beetle species composition in forest fragments in Central Amazonia independently from each other (Didham 1997b, Didham et al. 1998a). He found indication that even forest fragments of 100 ha are too small to preserve an intact continuous forest beetle fauna and due to local extinction of some dominant species, and a number of rare species, these fragments are faunistically distinct from the continuous forest (Didham 1997b). He determines the minimum area needed to maintain an intact terrestrial invertebrate assemblage is possibly 500−1000 ha (Didham 1997b). However, while beetle species richness in his study is highest in one hectare fragments, the species composition similarity to continuous forest is lowest (on average seven per cent; 43 % between continuous forest sites), indicating the influx of numerous disturbed-area species (Didham 1997b). The fragments of Yala (1180 ha) and the Kisere Forest (420 ha) are probably still large enough to maintain at least most of the main forest species. And also none of the other forest plots investigated are smaller than 200 ha and therefore, influence of fragmentation is not yet recognisable, since biodiversity is not significantly reduced in these parts of the forest. Also species richness estimated for the study sites (ACE, ICE) do not allow clear predictions about the highest diversity per study site; even if differences in species diversity between study sites were recognisable in one season, they shifted most likely in the following seasons to different results and therefore, no clear trends can be given and interpretations cannot be generalised at all. So also influx of edge effects and fragmentation size area is not always similar in each season and is only partly useful to explain diversity patterns and species presence in fragments and near forest edges. As stated by Murcia (Murcia 1995), edge effects are considerably more complex than previously thought and unusual variations in edge response may not be merely chaotic changes in the environment, but studies of edge effects should be wary of assuming that such effects change monotonically with distance from the forest edge.

Interspecific competition versus predator-prey interactions
If the abundance and diversity structure of beetles is only partly influenced by host specificity, seasonality, fragmentation and different forest types, what are the main

driving mechanisms for distribution patterns and biodiversity in this forest? Interspecific competition is not of great importance for phytophagous and especially for folivorous insects (Lawton & Strong 1981, Cornell 1985, Jermy 1985, Strauss 1988, Boecklen & Price 1991). Only a small proportion of highly specialized species, which occur in the tropics, probably compete for resources, especially if they feed on low-growing plants, e.g. larvae of *Heliconius* on *Passiflora* (Benson 1978). It is recorded, that arboreal, phytophagous insects in temperate as well as in tropic regions use only a small proportion of the available leaves (for temperate regions: e.g. Reichle et al. 1973, Southwood et al. 1982). This proportion is 6.0 % during the dry season and 18.0 % during the wet season in a tropical forest in Panama (Aide 1993), 5.0 % in Guyana (Sterck et al. 1992) and 5.2 to 10.9 % in Cameroon (Basset et al. 1992). In the studies of Schowalter & Ganio (2003) leaf area reduction by herbivores never exceeded 13.0 % and although Lowman (1992) found a relatively high proportion of 14.6 to 27.0 % of feeding damage on a common tree species in an Australian rain forest, there is no evidence that this particular food is limited and that competition between phytophagous species is necessary or takes place (cf. Grant 1986). It seems that interspecific competition is only of importance, if the resources are strongly limited, e.g. of highly adapted parasitoid insects (Pschorn-Walcher 1985) or miners and seed-feeders (Denno et al. 1995), but not of herbivore insects. It cannot be proved finally, if either food or places for oviposition, mating and development of larvae and pupae are limited by the vegetation, but after all what we know nowadays, it is not obvious and at least quite unlikely.

The occurrence of calamities of herbivores probably causes competition, but this is usually the fact in disturbed habitats or in plantations and this is not yet recorded in virgin tropical forests. This biome is characterized by small population densities of phytophagous and other insects and this fact would also exclude interspecific competition (cf. Chesson 1990). In the present study a total of 1023 species could be found on 192 trees investigated and 440 species of them are represented by one specimen only (about 43 % singletons) and 787 species are represented by less than ten individuals (about 77 %). There is no evidence for interspecific competition between species of any trophic guild with such small population densities. The distribution of individuals of rare species in time and space is generally unpredictable and is driven by chaotic factors (Vandermeer 1982). The dynamics and dispersal of insect populations is very heterogenic (Kareiva 1986, 1990) and long term studies in Panama from Wolda (1992b) show, that the population density of insects species, which at first could be found in large amounts, are extremely and irregularly fluctuating between few years. This fluctuation of abundance is also unpredictable and happens without any obvious regulating mechanisms (Wolda 1992b). As a result, neither successional stages nor a

climax community can emerge, quite similar to the present results, where abundances of species were also irregularly fluctuating between the seasons.

More important than interspecific interactions are probably predator-prey interactions in the tropics. Turchin et al. (1999) demonstrated the existence of predator-driven population cycles in canopy arthropods in an experiment using predator exclusion, showing that survival rates of the southern pine beetle *Dendroctonus frontalis* (Scolytinae) were significantly greater when protected from predators than when exposed. Predator-prey interactions are absolutely suited to explain the high diversity in the tropics, since both specialised and generalised predators (parasites and parasitoid species included) should use the most abundant prey more frequently. Specialists are probably specialised on abundant prey and generalists should capture abundant prey with a higher probability. This could explain the conditions in the tropics and low population densities and dispersal of species by chance without any constant equilibrium might be caused by a particular predation pressure (Caswell 1978). Some works on arthropod communities in tropical rain forests confirm this assumption and show the high dominance of carnivore ants with high impact as top predators on the abundance and composition of other arthropods (Strong 1982, Stork 1991, Wagner 2002). The proportion of Formicidae in the present study is certainly lower, but parasitoid Hymenoptera could be found more frequently than in other studies (see also Wagner 1997 for montane rain forests). The proportion of predators (including ants, spiders and parasitoid Hymenoptera) in the assemblages of the present study is quite high and although the composition of the predacious guild was changing during field work, the total percentages of this guild were largely constant (28.4 and 29.7 % for both wet seasons, 35.9 and 37.1 % for both dry seasons, Appendix 2−5). If this is not a chance effect, it could explain the quite similar faunal composition and percentages of arthropods collected during both wet and both dry seasons (Fig. 10, p. 31), since generalistic ants as well as specialised parasitoids restrict the population densities of most other arthropods by predator-prey interactions in a constant, but still unpredictable way.

Finally: stochastic or deterministic equilibrium models?

Besides interspecific competition and predator-prey interactions, of course, physical, respectively abiotic factors influence the distribution patterns in biocoenoses. Since these factors (such as light, levels of ultraviolet, rainfall, humidity and the condition and nitrogen balance of the soil) are also largely unpredictable, the structural characters of a biocoenosis are not constant and also lead to community disequilibrium and stochasticity in population densities (Grossman et al. 1982, Davis 1986). Not only the structure, but also the colonisation and recolonisation of habitats is unpredictable, since

it is dependent of the distribution of species, which is again driven by chance, like for instance the dispersal of tree species in tropical forests (Hubbell & Foster 1986). In this case also the size of the local species pool is of importance, because the more species potentially are able to colonise a habitat, the less predictable becomes the structure of a local community.

In conclusion, there are complex interactions between beetle taxa and their environment, influenced by seasonality, host specificity, forest type, fragmentation, edge effects and abiotic factors. In addition arthropod communities in the tropics usually are in disequilibrium, i.e. most of the species are rare and distributed by chance. The faunal and floral composition of tropical forests is driven by chance effects, unpredictability and stochasticity and species interactions are probably even more influenced by predator-prey interactions instead of fragmentation and degradation of forest habitats. It has been shown that forest fragmentation and degradation affects biodiversity (e.g. Saunders et al. 1991, Turner 1996, Didham 1997b, Didham et al. 1998a, Tabarelli et al. 1999, Debinski & Holt 2000, Laurance et al. 2002) but the isolated fragments in Yala and Kisere Forest do not show any significant species loss. They are probably still large enough to maintain approximately similar species numbers like the ones of the main forest; however, just the smaller forest patches in the main forest, namely Colobus Trail and Isiukhu River, are − despite good governmental protection − highly endangered by the influx of edge specialist species and accordingly more susceptible to forest species extinction, because the invasion of forest edges by disturbed-habitat species is of mixed fortune for forest fragments: edge invertebrates may displace some interior forest species by competition or predation (Didham 1997b), but equally, high abundance and biomass of invertebrates provides an increased food supply for many vertebrate and invertebrate predators (Malcolm 1997). Furthermore, the increasing species numbers due to edge influx causes difficulties in assessment of biodiversity. Comparisons of the fauna of different habitats are very difficult, because the proportion of forest core area species in assemblages is unknown. For that reason an establishment of indicator species for monitoring of changes in forest habitats would be important, especially since the proximate, mechanistic causes of population decline and extinction in habitat fragments are still largely conjecture (Didham 1997b).

The presented results show impressively that beetle assemblages are influenced by many biotic and abiotic factors in different ways and both species numbers and abundances are fluctuating from season to season without any visible pattern. This emphasizes the necessity and importance of long term studies and monitoring; otherwise no useful statements about the assessment of biodiversity in forests and forest fragments can be made. As stressed by Didham (Didham 1997b), such studies

should not only include the process of fragmentation itself, but also studies on area effects, edge effects, shape of fragments, the degree of spatio-temporal isolation and the degree of habitat connectivity to the main forest. So, certainly more investigations are necessary, but the link of the present results with other BIOTA East Africa sub-project studies will hopefully reveal more progress in studying the mechanisms that regulate and maintain the coexistence of animal and plant species in Kakamega Forest and are probably able to illuminate a fraction of the complex processes emanating from fragmentation.

5. Summary

At five different study sites in Kakamega Forest, a tropical wet forest in western Kenya, the canopy dwelling arthropod fauna of two common tree species was collected, using the insecticide fogging method. Three study sites were situated within the main forest (Colobus Trail, Isiukhu River and Busambuli River), and two were situated in isolated fragments of 420 ha size (Kisere Forest) and 1200 ha size (Yala River). Eight trees ("collecting unit") of *Teclea nobilis* (Rutaceae) were investigated at each site in the main forest and in the southern fragment. In Kisere and additionally also at Colobus Trail each of eight trees of *Heinsenia diervilleoides* (Rubiaceae) were fogged. Field work was conducted at four periods, two times during the wet season (October 2001 and 2002) and two times during the dry season (January 2002 and 2003).

The assemblages of arthropods were sorted to major groups and counted. Beetles were additionally allocated to morpho-types. The beta diversity was calculated with the Morisita-Horn Index. The beetle fauna was analysed with respect to guild structure; the guilds are predacious beetles, mycetophagous beetles and phytophagous leaf beetles and weevils.

A total canopy volume of approximately 1700 m³ was exploited and a total of 234,778 arthropods were collected. The most abundant group was Formicidae with more than 36,000 individuals (14.85 %). Then next abundant group was Diptera with about 35,500 individuals (14.56 %), parasitoid Hymenoptera with about 31,000 individuals (12.72 %), sap-sucking Homoptera with 26,500 individuals (10.90 %) and beetles with 24,300 individuals (9.97 %). A comparison of abundances shows that most of the taxa are more frequent during the rainy season. Differences of abundances between study sites were certainly visible, but fluctuated in a chaotic way between seasons. The arthropod community is only slightly influenced by fragmentation and degradation of forest habitats. Seasonality, predator-prey interactions and unpredictable dispersal by chance are probably more important for the distribution and presence of major groups.

A total of 1113 beetle larvae and 23,187 adult beetles were collected, which were allocated to 1023 morpho-types. The most abundant taxon was Corylophidae with 4081 individuals (17.6 %), followed by Staphylinidae (3598 ind., 15.52 %), Apionidae (3159 ind., 13.62 %), Curculionidae (2676 ind., 11.54 %) and Chrysomelidae (2565 ind., 11.06 %). The most species rich groups were Staphylinidae with 139 species, Chrysomelidae with 134 species and Curculionidae with 115 species. The beetle fauna was most diverse at Busambuli River, followed by the Yala fragment and Isiukhu River. The assemblages at Colobus Trail and in Kisere Forest revealed less species.

However, abundance and diversity of beetles was shifting from one season to another and the most diverse beetle fauna could be found each time at another site. Due to these fluctuations and the high proportion of singletons, no significant trends for the diversity of each forest habitat were recognisable.

A total of 4157 beetle individuals allocated to 179 species belong to predacious taxa. Remarkable is the different species composition during dry and wet seasons. The increased abundances of many species during the rainy season can be explained by favourable climatic conditions or a predator-prey relationship, since potential prey was also most abundant at this time.

A total of 4578 mycetophagous beetles were allocated to 54 species. Differences of diversity between study sites as well as between wet and dry seasons were hardly visible. Increased offer of fungi and accordingly increased humidity conditions led to high population densities.

A total of 2565 leaf beetles were allocated to 134 species. About 16 % of the species (singletons excluded) were host plant specific, since they were exclusively associated with only one of both tree species investigated; about three per cent (singletons excluded) of the species were forest habitat specific. Decreasing numbers of species in fragments could not be proved. High species numbers and low faunal overlap at Colobus Trail and Isiukhu River pointed to the high influence of edge effects and influx of forest edge species, due to their adjacent secondary habitats and not to an undisturbed, primary-like habitat with high proportions of rare species and unpredictability of species distribution.

With 5835 specimens, weevils were the most abundant beetle group. They were allocated to 128 species; about eight per cent of them were host plant specific, about five per cent forest habitat specific. High beta-diversity indices showed high similarities of faunal composition within a forest type. Differences between study sites were not remarkable.

In conclusion, there are (partly significant) differences of diversity and abundances of beetles between main forest and fragments. Results of all taxa investigated are fluctuating in each season without any visibly pattern. A decline in species richness in both fragments is not visible, obviously they are still large enough to maintain most of the forest species. At two sites with adjacent open grassland (Colobus Trail and Isiukhu River), edge effects are visible, since the fauna included further "non-forest" species, which leads to increased species numbers by higher dynamics of disturbed habitats.

The distribution of arthropods, especially of beetles, at different sites of Kakamega Forest is mainly based on stochastic events and predator-prey interactions, while fragmentation, forest degradation and interspecific competition have low influence.

Zusammenfassung

In fünf verschiedenen Untersuchungsflächen im Kakamega Forest, einem tropischen Regenwald im Westen Kenias, wurde die Arthropodenfauna von zwei häufigen, kleinwüchsigen Baumarten mit der Insektizid-Nebelmethode erfasst. Drei der Untersuchungsflächen lagen im Hauptwald (Colobus Trail, Isiukhu River und Busambuli River), zwei in vom Hauptwald isolierten Fragmenten von etwa 420 ha (Kisere Forest) und 1200 ha Größe (Yala River). An allen Standorten im Hauptwald und im südlichen Fragment wurden jeweils acht Bäume von *Teclea nobilis* (Rutaceae) untersucht. Da im nördlichen Fragment keine geeigneten Bäume dieser Baumart gefunden werden konnten, wurde eine weitere Baumart zu der Untersuchung hinzugezogen und acht Bäume von *Heinsenia diervilleoides* (Rubiaceae) benebelt. Zum besseren Vergleich wurden weitere acht Bäume dieser Art am Colobus Trail untersucht. Die Benebelung der insgesamt 48 Bäume wurde zweimal während der Regenzeit (Oktober 2001 und 2002) und zweimal während der Trockenzeit (Januar 2002 und 2003) durchgeführt.

Die erfassten Arthropoden wurden nach Großgruppen sortiert und ausgezählt, die Käfer zusätzlich Morphotypen zugeordnet. Mit diesen Daten waren statistische Analysen und die Berechnung von Diversitätsindices möglich. Von vier ausgewählten trophischen Käfergilden wurden neben diesen Berechnungen zusätzlich noch Rarefaction-Kurven, Korrespondenz- und Cluster-Analysen berechnet, die beta-Diversität wurde mit Hilfe des Morisita-Horn Index ermittelt. Die vier Gilden waren Prädatoren, mycetophage Käfer, Blattkäfer und die ebenfalls phytophagen Rüsselkäfer.

In einem eingenebelten Kronenvolumen von insgesamt etwa 1700 m³ wurden 234.778 Arthropoden erfasst. Ameisen waren mit über 36.000 Vertretern und 14,85 % die häufigste Gruppe. Danach folgten Dipteren mit knapp 35.500 Individuen (14,56 %), parasitische Hymenopteren mit etwa 31.000 Individuen (12,72 %), pflanzensaugende Homopteren mit etwa 26.500 Individuen (10,90 %) und Käfer mit 24.300 Vertretern (9,97 %) als die fünft-häufigste Gruppe. Ein Vergleich der Abundanzen zeigte, dass die meisten Taxa während der Regenzeit häufiger waren als in der Trockenzeit. Unterschiede von Abundanzen zwischen den Untersuchungsflächen konnten zwar in den jeweiligen Sammlungszeiträumen beobachtet werden, ließen aber keinen eindeutigen Trend erkennen; weder Fragmentierung noch Konvertierung der Waldflächen in Kakamega Forest hatten einen offensichtlichen Einfluss auf die

Arthropodenfauna. Scheinbar waren vielmehr saisonale Unterschiede, Räuber-Beute Beziehungen, sowie die starke Zufallsverteilung von entscheidender Bedeutung und maßgeblich für das Vorkommen und die Häufigkeit der Taxa.

23.187 adulte Käfer konnten 1023 Morphotypen zugeordnet werden. Die häufigsten Taxa waren Corylophidae mit 4081 Individuen (17,6 %), gefolgt von Staphylinidae (3598 Ind., 15,52 %), Apionidae (3159 Ind., 13,62 %), Curculionidae (2676 Ind., 11,54 %) und Chrysomelidae (2565 Ind., 11,06 %). Die artenreichsten Taxa waren Staphylinidae mit 139 Arten, Chrysomelidae mit 134 Arten und Curculionidae mit 115 Arten. Die Käferfauna war insgesamt am Busambuli River am artenreichsten, gefolgt vom Yala Fragment und Isiukhu River. Die Aufsammlungen am Colobus Trail und im Kisere Forest waren nicht so ergiebig. Die Abundanzen und Artenzahlen fluktuierten jedoch von einer Saison zur nächsten. Signifikante Tendenzen zum Artenreichtum der einzelnen Waldflächen waren u.a. aufgrund des hohen Anteils an Arten, die nur ein einziges Mal gefunden wurden (Singletons), nicht erkennbar.

Die untersuchten Käfergilden zeigten unterschiedliche Verteilungsmuster. Bei den carnivoren Käfern wurden 4157 Individuen 179 Arten zugeordnet, von denen 70 nur einmalig gefunden wurden. Auffällig war die unterschiedliche Artenzusammensetzung während der Trocken- und Regenzeit. Die Häufigkeit der meisten Arten während der Regenzeit, könnte durch günstigere klimatische Bedingungen oder Räuber-Beute Beziehungen erklärt werden, da auch die potenzielle Beute in dieser Zeit am häufigsten war.

Die 4578 mycetophagen Käfer wurden 54 Arten zugeordnet. Unterschiede zwischen den Untersuchungsflächen, sowie zwischen Regen- und Trockenzeiten waren kaum erkennbar. Die hohen Populationsdichten können durch ein erhöhtes Vorkommen an Pilzen und eine dementsprechend feuchtere Umgebung erklärt werden, die diese Käfer aufgrund ihrer Größe bevorzugen dürften.

Die 2565 Blattkäfer verteilten sich auf 134 Arten. Während der Trockenheit konnten mehr Individuen gefunden werden. Etwa 16 % der Arten (exklusive Singletons) waren wirtspflanzenspezifisch, da sie ausschließlich an einer von beiden untersuchten Baumarten gefunden wurden, etwa drei Prozent der Arten waren spezifisch für einen Waldtyp. Ein signifikanter Rückgang von Artenzahlen in den untersuchten Fragmenten konnte nicht nachgewiesen werden. Hohe Artenzahlen bei geringer Faunenüberlappung am Colobus Trail und Isiukhu River deuteten aufgrund der Lage eher auf Randeffekte und Vermischung von Waldarten und Arten, die von offeneren Habitaten einwandern,

hin, als auf ein ungestörtes Habitat, das von einem hohen Anteil seltener Arten und Unvorhersagbarkeit ihrer Verbreitung geprägt ist.

Rüsselkäfer waren mit 5835 Vertretern die individuenreichste Gruppe. Sie wurden 128 Arten zugeordnet, etwa acht Prozent von ihnen waren wirtspflanzenspezifisch. Die beta-Diversitätsindices belegten eine hohe Übereinstimmung innerhalb eines Waldtyps. Auch in dieser Gruppe konnten keine signifikanten Unterschiede zwischen den Untersuchungsflächen gefunden werden.

Insgesamt kann man sagen, dass zwar (zum Teil signifikante) Unterschiede in Diversität und Abundanz von Käfern zwischen Hauptwald und Fragmenten bestehen, aber diese lassen keine allgemeingültigen Aussagen zu. Einen Artenrückgang konnte man in keinem der beiden Fragmente beobachten. Offensichtlich hat ihre Größe noch nicht einen kritischen Grenzwert unterschritten und die meisten Waldarten können weiterhin beherbergt werden. Lediglich in den beiden Untersuchungsflächen, die sehr nah an der Grenze zum benachbarten Grasland lagen (Colobus Trail und Isiukhu River) konnten „edge effects" beobachtet werden, da die Fauna durch viele Nicht-Waldarten geprägt wurde. Dies führte z.T. sogar zu erhöhten Artenzahlen, was sich durch eine erhöhte Dynamik in gestörten Lebensräumen erklären lässt. Die Verteilung von Arthropoden, insbesondere die der Käfer, dürfte im Wesentlichen auf Zufallseffekte und Prädationsdruck beruhen, während Fragmentierung, Degradierung des Waldes und interspezifische Konkurrenz in den untersuchten Gebieten des Kakamega Forest bis jetzt nur eine untergeordnete Rolle spielen dürften.

6. References

ACHARD, F., EVA, H. D., STIBIG, H.-J., MAYAUX, P., GALLEGO, J., RICHARDS, T. & MALINGREAU, J.-P. (2002). Determination of Deforestation Rates of the World´s Humid Tropical Forests. *Science* **297,** 999−1002.

ACHTZIGER, R., NIGMANN, U. & ZWÖLFER, H. (1992). Rarefaction-Methoden und ihre Einsatzmöglichkeiten bei der zooökologischen Zustandsanalyse und Bewertung von Biotopen. *Zeitschrift für Ökologie und Naturschutz* **1,** 89−105.

ADIS, J. (1988). On the abundance and density of terrestrial arthropods in central Amazonian dryland forests. *Journal of tropical Ecology* **4,** 19−24.

ADIS, J., LUBIN, Y. D. & MONTGOMERY, J. J. (1984). Arthropods from the canopy of inundated and terra firme forests near Manaus, Brazil, with critical considerations on the pyrethrum-fogging technique. *Studies on Neotropical Fauna and Environment* **4,** 223−236.

ADIS, J., PAARMANN, W., DA FONSECA, C. R. V. & RAFAEL, J. A. (1997). Knockdown efficiency of natural pyrethrum and survival rate of living arthropods obtained by canopy fogging in Central Amazonia. In *Canopy Arthropods.* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 67−81. Chapman & Hall, London.

AIDE, T. M. (1992). Dry season leaf production: an Escape from Herbivory. *Biotropica* **24,** 532−537.

AIDE, T. M. (1993). Patterns of leaf development and herbivory in a tropical understorey community. *Ecology* **74,** 455−463.

AIDE, T. M. & ZIMMERMAN, J. K. (1990). Patterns of insect herbivory, growth, and survivorship in juveniles of a neotropic liana. *Ecology* **71,** 1412−1421.

ALLISON, A., SAMUELSON, G. A. & MILLER, S. E. (1993). Paterns of beetle species diversity in New Guinea rain forest as revealed by canopy fogging: Preliminary findings. *Selbyana* **14,** 16−20.

ALTHOF, A., FISCHER, E., KILLMANN, D. & MWACHALA, G. (2003). Influence of natural and anthropogenic fragmentation on diversity of flora and vegetation in upland and montane rainforests of East Africa. In *Sustainable use and conservation of biological diversity - A challange for society. Symposium Report: Part A*, pp. 108−109, Berlin.

ÅS, S. (1993). Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography* **16,** 219−228.

ASKEW, R. R. (1990). Species diversity of hymenopteran taxa in Sulawesi. In *Insects and the Rain Forests of South East Asia (Wallacea).* (eds. W. J. Knight and J. D. Holloway), pp. 255−260. The Royal Entomological Society of London, London.

BACH, C. (1990). Plant successional stage and insect herbivory: Flea beetles on sand-dune willow. *Ecology* **71,** 598−609.

BALMFORD, A., MOORE, J. L., BROOKS, T. M., BURGESS, N., HANSEN, L. A., WILLIAMS, P. & RAHBECK, C. (2001). Conservation conflicts across Africa. *Science* **291,** 2619.

BANERJEE, B. (1987). Can leave aspect affect herbivory? A case study with tea. *Ecology* **68,** 839−843.

BARKER, M. G. & PINARD, M. A. (2001). Forest canopy research: sampling problems, and some solutions. *Plant Ecology* **153,** 23−38.

BARRIOS, H. (2003). Insect herbivores feeding conspecific seedlings and trees. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 282−290. University Press, Cambridge.

BARTHLOTT, W., BIEDINGER, M., BRAUN, G., FEIG, F., KIER, G. & MUTKE, J. (1999). Terminological and methodological aspects of the mapping and analysis of global biodiversity. *Acta Botanica Fennica* **162,** 103−110.

BASSET, Y. (1992a). Host-specificity of arboreal and free-living insect herbivores in rain forests. *Biological Journal of the Linnean Society* **47,** 115−133.

BASSET, Y. (1992b). Influence of leaf traits on the spatial distribution of arboreal arthropods within an overstorey rainforest tree. *Ecological Entomology* **17,** 8−16.

BASSET, Y. (1996). Local communities of arboreal herbivores in Papua New Guinea: Predictors of insect variables. *Ecology* **77,** 1906−1919.

BASSET, Y. (2001a). Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia* **129,** 253−260.

BASSET, Y. (2001b). Invertebrates in the canopy of tropical rain forests: how much do we really know? *Plant Ecology* **153,** 87−107.

BASSET, Y., ABERLENC, H. P. & DELVARE, G. (1992). Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. *Ecological Entomology* **17,** 310−318.

BASSET, Y. & ARTHINGTON, A. H. (1992). The arthropod community of an Australian rainforest tree: Abundance of component taxa, species richness and guild structure. *Australian Journal of Ecology* **17,** 89−98.

BASSET, Y., CHARLES, E. & NOVOTNY, V. (1999). Insect herbivores on parent trees and conspecific seedlings in a rain forest in Guyana. *Selbyana* **20,** 146−158.

BASSET, Y., HAMMOND, P. M., BARRIOS, H., HOLLOWAY, J. D. & MILLER, S. E. (2003). Vertical stratification of arthropod assemblages. In *Arthropods in Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 17−27. University Press, Cambridge.

BASSET, Y. & KITCHING, R. L. (1991). Species number, species abundance and body length of arboreal arthropods associated with an Australian rainforest tree. *Ecological Entomology* **17,** 310−318.

BASSET, Y., SPRINGATE, N. D., ABERLENC, H. P. & DELVARE, G. (1997). A review of methods for sampling arthropods in tree canopies. In *Canopy Arthropods* (eds. Nigel E. Stork, J. Adis and R. K. Didham), pp. 27−52. Chapman & Hall, London.

BEAVER, R. A. (1979a). Host specificity in temperate and tropical animals. *Nature* **281,** 139−141.

BEAVER, R. A. (1979b). Non-equilibrium "island" communities: A guild of tropical bark beetles. *Journal of Animal Ecology* **48,** 987−1002.

BEENTJE, H. J. (1994). *Kenya trees, shrubs and lianas*. Majestic Printing Works Ltd., Nairobi.

BELLINGER, R. G., RAVLIN, F. W. & MCMANUS, M. L. (1989). Forest edge effects and their influence on Gypsy Moth (Lepidoptera: Lymantriidae) egg mass distribution. *Environmental Entomology* **18,** 840−843.

BENDER, D. J., CONTRERAS, T. A. & FAHRIG, L. (2003). Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* **79,** 517−533.

BENNUN, L. & NJOROGE, P. (1999). Important bird areas in Kenya. Nature Kenya, Nairobi.

BENSON, W. W. (1978). Resource partitioning in passione vine butterflies. *Evolution* **32,** 493−518.

BIERREGAARD, R. O., JR., GASCON, C., LOVEJOY, T. E. & MESQUITA, R. (2001). Lessons from Amazonia. The ecology and conservation of a fragmented forest. Yale University Press, New Heaven.

BIERREGAARD, R. O., LOVEJOY, T. E., KAPOS, V., SANTOS, A. A. & HUTCHINGS, R. W. (1992). The biological dynamics of tropical forest fragments. A prospective comparison of fragments and continous forest. *BioScience* **42,** 859−866.

BLACKETT, H. L. (1994). Forest Inventory Report No. 3. Kakamega. Forest Department / KIFCON, Kenya, Nairobi.

BOECKLEN, W. J. & PRICE, P. W. (1991). Nonequilibrial community structure of sawflies on arroyo willow. *Oecologia* **85,** 483−491.

BOWDEN, J., HAINES, I. H. & MERCER, D. (1976). Climbing Collembola. *Pedobiologia* **165,** 298−312.

BRAAKHEKKE, W. G. (1985). The significance of competition for plant diversity. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23,** 315−327.

BROADHEAD, E. & THORNTON, I. W. B. (1955). An ecological study of three closely related psocid species. *Oikos* **6,** 1−50.

BROADHEAD, E. & WOLDA, H. (1985). The diversity of Psocoptera in two tropical forests in Panama. *Journal of Animal Ecology* **54,** 739−754.

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, K. S., JR. & HUTCHINGS, R. W. (1997). Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. In *Tropical forest remnants: ecology, management and conservation of fragmented communities.* (eds. W. F. Laurance and R. O. Bierregaard, Jr.), pp. 91−110. University of Chicago Press, Chicago, Illinois, USA.

BROWN, M. V., JR. (1973). A comparison of the Hylean and Congo West African rain forest ant faunas. In *Tropical forest ecosystems in Africa and South America: a comparative review.* (eds. B. J. Meggers, E. S. Ayensu and W. D. Duckworth), pp. 161−185. Smithsonian Institution Press, Washington D. C.

BROWN, S. & LUGO, A. E. (1990). Tropical secondary forests. *Journal of tropical Ecology* **6,** 1−31.

BROWN, V. K. & HYMAN, P. S. (1986). Successional communities of plants and phytophagous Coleoptera. *Journal of Ecology* **74,** 963−975.

BUSE, A. & GOOD, J. E. G. (1993). The effects of conifer forest design and management on abundance and diversity of rove beetles (Coleoptera: Staphylinidae): Implications for conservation. *Biological Conservation* **65,** 67−76.

CAMARGO, J. L. C. & KAPOS, V. (1995). Complex edge effects on soil-moisture and microclimate in central Amazonian forest. *Journal of tropical Ecology* **11,** 205−221.

CARAGLIO, Y., NICOLINI, E. & PETRONELLI, P. (2001). Observations on the links between the architecture of a tree (*Dicorynia guianensis* Amshoff) and Cerambycidae activity in French Guiana. *Journal of tropical Ecology* **17,** 459−463.

CASIDA, J. H. & QUISTAD, G. B. (1995). *Pyrethrum flowers: Production, chemistry, toxicology, and uses.* Oxford University Press, Oxford.

CASWELL, H. (1976). Community structure: A neutral model analysis. *Ecological Monographs* **46,** 327−354.

CASWELL, H. (1978). Predator mediated coexistence: A non-equilibrium model. *American Naturalist* **112,** 127−154.

CATES, R. G. (1980). Feeding patterns of monophagous, oligophagous and polyphagous insect herbivores: The effect of resource abundance and plant chemistry. *Oecologia* **46,** 22−31.

CHAO, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11,** 265−270.

CHAO, A. & LEE, S. M. (1992). Estimating the number of classes via sample coverage. *Journal of the American Statistical Association* **87,** 210−217.

CHAO, A., MA, M. C. & YANG, M. C. K. (1993). Stopping Rules and Estimation for Recapture Debugging with Unequal Failure Rates. *Biometrika* **80,** 193−201.

CHAZDON, R. L., COLWELL, R. K., DENSLOW, J. S. & GUARIGUATA, M. R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies.* (eds. F. Dallmeier and J. A. Comiskey), pp. 285−309. Parthenon Publishing, Paris.

CHESSON, P. L. (1990). Geometry, heterogeneity and competition in variable environments. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **330,** 165−173.

CINCOTTA, R. P., WISNEWSKI, J. & ENGELMAN, R. (2000). Human population in the biodiversity hotspots. *Nature* **404,** 990−992.

CODY, M. L. (1993). Bird diversity components within and between habitats in Australia. In *Species diversity in ecological communities: historical and geographical perspectives.* (eds. R. E. Ricklefs and D. Schluter), pp. 147−158. University of Chicago Press, Chicago, Illinois, USA.

COLEY, P. D. & AIDE, T. M. (1991). Comparison of herbivory and plant defences in temperate and tropical broad-leaved forests. In *Plant-animal interactions.* (eds. P. W. Price, Th. M. Lewinsohn, G. W. Fernandes and W. W. Benson), pp. 25−49. Wiley & Sons, New York etc.

COLEY, P. D. & BARONE, J. A. (1996). Herbivory and plant defences in tropical forests. *Annual Review of Ecology and Systematics* **27,** 305−335.

COLLINS, N. M. (1992). Introduction. In *The Conservation Atlas of Tropical Forests-Africa.* (eds. Jeffrey A. Sayer, Caroline S. Harcourt and N. Mark Collins), pp. 9−16. Macmillan Publishers Ltd., United Kingdom.

COLWELL, R. K. (1997). EstimateS: Statistical estimation of species richness and shared species from samples. Version 6.0b1. http://viceroy.eeb.uconn.edu/estimates.

COLWELL, R. K. & CODDINGTON, J. A. (1994). Estimating Terrestrial Biodiversity through Extrapolation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **345,** 101−118.

CONNOR, E. F. & SIMBERLOFF, D. (1979). The assembly of species communities: Chance or competition. *Ecology* **60,** 1132−1140.

CORNELL, H. V. (1985). Species assemblages of cynipid gall wasps are not saturated. *American Naturalist* **126,** 565−569.

CORNELL, H. V. & LAWTON, J. H. (1992). Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61,** 1−12.

CROWSON, R. A. (1967). *The natural classification of the families of Coleoptera.* Classey, Middlesex.

CSIRO. (1991a). The Insects of Australia, Vol. 1, pp. 542. Melbourne University Press, Carlton.

CSIRO. (1991b). The Insects of Australia, Vol. 2, pp. 543−1137. Melbourne University Press, Carlton.

DAILY, G. C. & EHRLICH, P. R. (1995). Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation* **4,** 35−55.

DAVIDSON, D. W. (1997). The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society* **61,** 153−181.

DAVIDSON, D. W. (1998). Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology* **23,** 484−490.

DAVIDSON, D. W., COOK, S. C., SNELLING, R. R. & CHUA, T. H. (2003). Explaining the Abundance of Ants in Lowland Tropical Rainforest Canopies. *Science* **300,** 969−972.

DAVIES, J. G., STORK, N. E., BRENDELL, M. J. D. & HINE, S. J. (1997). Beetle species diversity and faunal similarity in Venezuelan rainforest tree canopies. In *Canopy Arthropods.* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 85−103. Chapman & Hall, London.

DAVIS, M. B. (1986). Climatic instability, time lags, and community disequilibrium. In *Community ecology.* (eds. J. M. Diamond and T. J. Case), pp. 269−284. Harper & Row, New York etc.

DE DIJN, B. P. E. (2003). Vertical stratification of flying insects in a Surinam lowland rainforest. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 110−122. University Press, Cambridge.

DE WILDE, J. W. (1969). Effects of host plant age on phytophagous insects. *Entomol. Exp. Appl.* **12,** 714−720.

DEBINSKI, D. M. & HOLT, R. D. (2000). A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14,** 342−355.

DEN BOER, P. J. (1985). Exclusion, competition or coexistence? A question of testing the right hypothesis. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23,** 259−274.

DEN BOER, P. J. (1990). The survival value of dispersal in terrestrial arthropods. *Biological Conservation* **54,** 175−192.

DENLINGER, D. L. (1980). Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica* **12,** 100−106.

DENLINGER, D. L. (1986). Dormancy in tropical insects. *Annual Review of Entomology* **31,** 239−264.

DENNO, R. F., MCCLURE, M. S. & OTT, J. R. (1995). Interspecific interactions in phytophagous insects: Competition reexamined and resurrected. *Annual Review of Entomology* **40,** 297−331.

DERRAIK, J. G. B., CLOSS, G. P., DICKINSON, K. J. M., SIRVID, P., BARRATT, B. I. P. & PATRICK, B. H. (2002). Arthropod morphospecies versus taxonomic species: a case study with Araneae, Coleoptera, and Lepidoptera. *Conservation Biology* **16,** 1015−1023.

DIAMOND, J. M. (1972). Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proceedings of the National Academy of Sciences of the U.S.A.* **69,** 3199−3203.

DIDHAM, R. K. (1997a). Dipteran tree-crown assemblages in a diverse southern temperate rainforest. In *Canopy Arthropods* (eds. Nigel E. Stork, J. Adis and R. K. Didham), pp. 320−343. Chapman & Hall, London.

DIDHAM, R. K. (1997b). An overview of invertebrate responses to forest fragmentation. In *Forests and Insects.* (eds. A. D. Watt, Nigel E. Stork and M. D. Hunter), pp. 303−320. Chapman & Hall, London.

DIDHAM, R. K., HAMMOND, P. M., LAWTON, J. H., EGGLETON, P. & STORK, N. E. (1998a). Beetle species responses to tropical forest fragmentation. *Ecological Monographs* **68,** 295−323.

DIDHAM, R. K., LAWTON, J. H., HAMMOND, P. M. & EGGLETON, P. (1998b). Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **353,** 437−451.

DIDHAM, R. K. & SPRINGATE, N. D. (2003). Determinants of temporal variation in community structure. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 28−39. University Press, Cambridge.

DIXON, A. F. G., KINDLMANN, P., LEPS, J. & HOLMAN, J. (1987). Why there are so few species of aphids, especially in the tropics. *American Naturalist* **129,** 580−592.

DUELLI, P., STUDER, M., MARCHAND, I. & JAKOB, S. (1990). Population movements of arthropods between natural and cultivated areas. *Biological Conservation* **54,** 193−207.

ELLIOTT, M., JANES, N. F. & POTTER, C. (1978). The future of pyrethroids in insect control. *Annual Review of Entomology* **23,** 443−469.

ELTON, C. S. (1973). The structure of invertebrate populations inside neotropical rain forests. *Journal of Animal Ecology* **42,** 55−104.

EMMERTON, L. (1991). Utilisation of Kakamega Forest by adjacent households. Kenya Indigenous Forests Conservation Program. Keruna Forest Station, Nairobi.

ERWIN, T. L. (1982). Tropical forests: Their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36,** 74−75.

ERWIN, T. L. (1983). Tropical forest canopies: The last biotic frontier. *Bulletin of the entomological Society of America* **30,** 14−19.

ERWIN, T. L. (1989). Canopy arthropod biodiversity: a chronology of sampling techniques and results. *Revista Peruana de Entomología* **32,** 71−77.

ERWIN, T. L. & SCOTT, J. C. (1980). Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Luehea seemannii* Triana & Planch in the Canal Zone of Pananma. *The Coleopterists Bulletin* **34,** 305−322.

FAHRIG, L. & MERRIAM, G. (1994). Conservation of fragmented populations. *Conservation Biology* **8,** 50−59.

FAO. (2003). African forest: a view to 2020. In *FAO*, Rome.

FARRELL, B. D., DUSSOURD, D. E. & MITTER, C. (1991). Escalation of plant defense: do latex and resin canals spur plant diversification? *American Naturalist* **138,** 881−900.

FARRELL, B. D., MITTER, C. & FUTUYMA, D. J. (1992). Diversification at the insect-plant interfaces. Insights from phylogenetics. *Bio Science* **42,** 34−42.

FJELDSA, J. & LOVETT, J. C. (1997). Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation* **6,** 325−346.

FLOREN, A., BIUN, A. & LINSENMAIR, K. E. (2002). Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia* **131,** 137−144.

FLOREN, A. & LINSENMAIR, K. E. (1994). Zur Diversität und Wiederbesiedlungsdynamik von Arthropoden auf drei Baumarten in einem Regenwald in Sabah, Malaysia. *Andrias* **13,** 23−28.

FLOREN, A. & LINSENMAIR, K. E. (1997). Diversity and recolonisation dynamics of selected arthropod groups on different tree species in a lowland rainforest in Sabah, Malaysia with special reference to Formicidae. In *Canopy Arthropods* (eds. Nigel E. Stork, J. Adis and R. K. Didham), pp. 344−381. Chapman & Hall, London.

FLOREN, A. & LINSENMAIR, K. E. (2001). The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. *Plant Ecology* **153,** 153−167.

FLOREN, A. & LINSENMAIR, K. E. (2003). How do beetle assemblages respond to anthropogenic disturbance? In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 190−197. University Press, Cambridge.

FLOWERS, R. W. (1991). Aggregations of Cassidinae (Chrysomelidae) in Santa Rosa and Guanacaste National Parks, Costa Rica. *Biotropica* **23,** 308−310.

FOWLER, S. V. (1985). Differences in insect species richness and faunal composition of birch seedlings, saplings and trees: The importance of plant architecture. *Ecological Entomology* **10,** 159−169.

FREUDE, H., HARDE, K. W. & LOHSE, G. A. (1964−1983). Die Käfer Mitteleuropas, Vol. 1−11. Goecke & Evers, Krefeld.

FREUND, W. & WAGNER, T. (2003). Revision of *Bonesioides* Laboissiere, 1925 (Coleoptera; Chrysomelidae; Galerucinae) from continental Africa. *Journal of Natural History* **37,** 1915−1976.

FRITH, C. B. & FRITH, D. W. (1985). Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology* **10,** 237−248.

FRITZ, R. S. & PRICE, P. W. (1988). Genetic variation among plants and insect community structure: Willows and sawflies. *Ecology* **67,** 1608−1618.

FUTUYMA, D. J. (1976). Food plant specialsiation and environmental predictability in Lepidoptera. *American Naturalist* **110,** 285−292.

GASTON, K. J. (1991a). Estimates of the Near-Imponderable: A Reply to Erwin. *Conservation Biology* **5,** 564−566.

GASTON, K. J. (1991b). The Magnitude of Global Insect Species Richness. *Conservation Biology* **5,** 283−296.

GASTON, K. J. (2000). Global patterns in biodiversity. *Nature* **405,** 220−227.

GILPIN, M. E. & SOULÉ, M. E. (1986). Minimal viable populations: process of species extinction. In *Conservation Biology: the science of scarcity and diversity.* (ed. M. E. Soulé), pp. 19−34. Sinauer, Sunderland, Massachusetts.

GODFRAY, H. C. J., LEWIS, O. T. & MEMMOT, J. (1999). Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **354,** 1811−1824.

GRANT, P. R. (1986). Interspecific competition in fluctuating environments. In *Community ecology.* (eds. J. M. Diamond and T. J. Case), pp. 173−191. Harper & Row, New York etc.

GROOMBRIDGE, B. & JENKINS, M. D. (2002). *World Atlas of biodiversity. Earth's living resources in the 21st century.* University of California Press, Berkeley.

GROSSMAN, G. D., MOYLE, P. B. & WHITAKER, J. O. (1982). Stochasticity in structural and functional characteristics of an Indianan stream fish assemblage: A test of community theory. *American Naturalist* **120,** 423−454.

GUERRERO, J. C. H., DA FONSECA, C. R. V., HAMMOND, P. M. & STORK, N. E. (2003). Seasonal variation of canopy arthropods in Central Amazon. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 170−175. University Press, Cambridge.

HADDOW, A. J. & CORBET, P. S. (1961). Entomological studies from a high tower in Mpanga Forest, Uganda. V. Swarming activity above the forest. *Transactions of the Royal Entomological Society of London* **113,** 284−300.

HALAJ, J., ROSS, D. W. & MOLDENCKE, A. R. (1997). Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* **109,** 313−322.

HALFFTER, G., FAVILA, M. E. & HALFFTER, V. (1992). A comparative study of the structure of the scarab guild in Mexican tropical rain forests and derived ecosystems. *Folia Entomológica Mexicana* **84,** 131−156.

HALME, E. & NIEMALÄ, J. (1993). Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* **30,** 17−30.

HAMILTON, A. C. (1992). History of forests and climate. In *The Conservation Atlas of Tropical Forests-Africa.* (eds. Jeffrey A. Sayer, Caroline S. Harcourt and N. Mark Collins), pp. 288. Macmillan Publishers Ltd., United Kingdom.

HAMMOND, P. M. (1990). Insect abundance in Dumoga-Bone National Park, North Sulawesi, with special reference to the beetle fauna of lowland rainforest in the Toraut region. In *Insects and the rainforest of South East Asia (Wallacea).* (eds. W. J. Knight and J. D. Holloway), pp. 197−254. Royal entomological Society of London, London.

HAMMOND, P. M. (1994). Practical Approaches to the Estimation of the Extent of Biodiversity in Speciose Groups. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **345,** 119−136.

HAMMOND, P. M., STORK, N. E. & BRENDELL, M. J. D. (1997). Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. In *Canopy Arthropods* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 184−223. Chapman & Hall, London.

HAYEK, L. C. & BUZAS, M. A. (1996). *Surveying natural populations*. Columbia University Press, New York.

HELLE, P. & MUONA, J. (1985). Invertebrate numbers in edges between clearfellings and mature forest in northern Finland. *Silva Fennica* **19,** 281−294.

HILL, M. O. (1973). Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology* **61,** 237−249.

HODKINSON, I. D. (1992). Global insect diversity revisited. *Journal of tropical Biology* **8,** 505−508.

HODKINSON, I. D. & CASSON, D. (1991). A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society* **43,** 101−109.

HORN, H. S. (1966). Measurement of "overlap" in comparative ecological studies. *American Naturalist* **100,** 419−424.

HORSTMANN, K., FLOREN, A. & LINSENMAIR, K. E. (1999). High species richness of Ichneumonidae (Hymenoptera) from the canopy of a Malaysian rain forest. *Ecotropica* **5,** 1−12.

HUBBELL, S. P. & FOSTER, R. B. (1986). Biology, chance, and history and the structure of tropical rain forest tree communities. In *Community ecology.* (eds. J. M. Diamond and T. J. Case), pp. 314−329. Harper & Row, New York etc.

HURLBERT, S. H. (1971). The non-concept of species diversity: A critique and alternative parameters. *Ecology* **52,** 577−586.

HUSTON, M. A. (1979). A general hypothesis of species diversity. *American Naturalist* **113,** 81−101.

HUSTON, M. A. (1994). *Biological Diversity. The coexistence of species on changing landscapes.* Cambridge University Press, Cambridge.

JACOBS, J. (1985). Konkurrenz und Einnischung - Hat Konkurrenz um Ressourcen eine evolutionsbiologische Bedeutung für die Artenmannigfaltigkeit der Tiere? *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23,** 243−258.

JACOBS, W. & RENNER, M. (1988). *Biologie der Insekten.* 2. Auflage. Gustav Fischer, Stuttgart.

JAENIKE, J. R. (1973). A steady model of genetic polymorphism on islands. *The American Naturalist* **107,** 793−795.

JAMES, F. C. & MCCULLOCH, C. E. (1990). Multivariate analysis in ecology and systematics: panacea or pandora's box? *Annual Review of Ecological Systematics* **21,** 129−166.

JANZEN, D. H. (1970). Herbivores and the number of tree species in tropical forests. *American Naturalist* **104,** 501−528.

JANZEN, D. H. (1980). Specificity of seed-eating beetles in a Costa Rican deciduous forest. *Journal of Ecology* **68,** 929−952.

JANZEN, D. H. & SCHOENER, T. W. (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical season. *Ecology* **49,** 96−110.

JERMY, T. (1985). Is there competition between polyphagous insects? *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23,** 275−285.

JERMY, T. (1994). Hypotheses on oligophagy: how far the case of the Colorado potato beetle supports them. In *Novel aspects of the biology of Chrysomelidae.* (eds. P. H. Jolivet, M. L. Cox and E. Petitpierre), pp. 127−139. Kluiver Academic Publishers, Dordrecht, etc.

JOLIVET, P. H. (1979). Les Chrysomelidae (Coleoptera) des *Citrus* et apparentes (Rutaceae) en zone tempérée et tropicale. *Bull. Soc. Linn. Lyon* **48,** 197−200, 249−256.

JOLIVET, P. H. (1986). *Insects and Plants.* E. J. Brill, Flora and Fauna Publishers, New York.

JOLIVET, P. H. & HAWKESWOOD, T. J. (1995). *Host-plants of chrysomelidae of the world.* Backhuys Publishers, Leiden.

KAPOS, V. (1989). Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of tropical Ecology* **5,** 173−185.

KAPOS, V., WANDELLI, E., CAMARGO, J. L. C. & GANADE, G. (1997). Edge-related changes in environment and plant responses due to forest fragmentation in Central Amazonia. In *Tropical forest remnants: ecology, management and conservation of fragmented communities.* (eds. W. F. Laurance and R. O. Bierregaard, Jr.). University of Chicago Press, Chicago, Illinois, USA.

KAREIVA, P. (1986). Patchiness, dispersal, and species interactions: Consequences for communities of herbivorous insects. In *Community ecology.* (eds. J. M. Diamond and T. J. Case), pp. 192−206. Harper & Row, New York etc.

KAREIVA, P. (1987). Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326,** 388−390.

KAREIVA, P. (1990). Population dynamics in spatially complex environments: Theory and data. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **330,** 175−190.

KIFCON. (1994). *Kakamega Forest - The official guide.* Kenya Indigenous Forest Conservation Programme, Nairobi.

KITCHING, R. L. & ARTHUR, M. (1993). The biodiversity of arthropods from Australian rainforest canopies: summary of projects and impact of drought. *Selbyana* **14,** 29−35.

KITCHING, R. L., HURLEY, K. L. & THALIB, L. (2003). Tree ralatedness and the similarity of insect assemblages: pushing the limits? In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 329−340. University Press, Cambridge.

KITCHING, R. L., MITCHELL, H., MORSE, G. & THEBAUD, C. (1997). Determinants of species richness in assemblages of canopy arthropods in rainforests. In *Canopy Arthropods* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 131−150. Chapman & Hall, London.

KOCH, K. (1992). *Die Käfer Mitteleuropas. - Ökologie, Bd. 3.* Goecke & Evers, Krefeld.

KÖHLER, J. & NAUMANN, C. M. (2003). Towards a sustainable use of East African rain forest systems: Analysis of biodiversity function and socio-economic drivers along gradients of degradation. In *Sustainable use and conservation of biological diversity - A challange for society. Symposium Report: Part A,* pp. 102−103, Berlin.

KOKWARO, J. O. (1988). Conservation status of the Kakamega Forest in Kenya - the easternmost relic of the equatorial rain forests of Africa. *Monographs in Systematic Botany of the Missouri Botanical Garden* **25,** 471−489.

KREBS, C. J. (1999). *Ecological Methodology*, second edition. Benjamin Cummings, Menlo Park.

KREMEN, C., COLWELL, R. K., ERWIN, T. L., MURPHY, D. D., NOSS, R. F. & SANJAYAN, M. A. (1993). Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* **7,** 796−808.

KRUESS, A. & TSCHARNTKE, T. (1994). Habitat fragmentation, species loss, and biological control. *Science* **264,** 1581−1584.

LANDSBERG, J. (1990). Dieback of rural eucalypts: the effect of stress on the nutritional quality of foliage. *Australian Journal of Ecology* **15,** 97−107.

LARSON, S. & OHMART, C. P. (1988). Leaf age and larval performance of the leaf beetle *Paropsis atomaria*. *Ecological Entomology* **13,** 19−24.

LASALLE, J. & GAULD, I. D. (1991). Parasitic Hymenoptera and the biodiversity crisis. *Redia* **74,** 315−334.

LAURANCE, W. F. (1991). Edge effects in tropical forest fragments: application of a model for the design of nature reserves. *Biological Conservation* **57,** 205−219.

LAURANCE, W. F. & BIERREGAARD, R. O., JR. (1997). Tropical forest remnants. Ecology, management and conservation of fragmented communities. The University of Chicago Press, Chicago.

LAURANCE, W. F., FERREIRA, L. V., RANKIN-DE MERONA, J. M. & LAURANCE, S. G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79,** 2032−2040.

LAURANCE, W. F., LOVEJOY, T. E., VASCONCELOS, H. L., BRUNA, E. M., DIDHAM, R. K., STOUFFER, P. C., GASCON, C., BIERREGAARD, R. O., LAURANCE, S. G. & SAMPAIO, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* **16,** 605−618.

LAURANCE, W. F. & YENSEN, E. (1991). Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* **55,** 77−92.

LAWRENCE, J. F. & BRITTON, E. B. (1991). Coleoptera. In *The Insects of Australia, Vol. 2.* (eds. CSIRO and Division of Entomology.), pp. 543−683. University College of London Press, London.

LAWTON, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology* **28,** 23−39.

LAWTON, J. H. (1991). Species richness, population abundances, and body size in insect communities: Tropical versus temperate comparisons. In *Plant-animal interactions.* (eds. P. W. Price, Th. M. Lewinsohn, G. W. Fernandes and W. W. Benson), pp. 71−89. Wiley & Sons, New York etc.

LAWTON, J. H. & SCHRÖDER, D. (1977). Effects of host plant type, size of geographic range and taxonomic isolation on number of insect species associated with British plants. *Nature* **265,** 137−140.

LAWTON, J. H. & STRONG, D. R. (1981). Community patterns and competition in folivorous insects. *American Naturalist* **118,** 317−337.

LEE, S. M. & CHAO, A. (1994). Estimating Population-Size Via Sample Coverage for Closed Capture-Recapture Models. *Biometrics* **50,** 88−97.

LINSENMAIR, K. E. (1990). Tropische Biodiversität: Befunde und offene Probleme. *Verhandlungen der deutschen zoologischen Gesellschaft* **83,** 245−261.

LOVEJOY, T. E. (1994). The quantification of biodiversity: an esoteric quest or a vital component of sustainable development? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **345,** 81−87.

LOVEJOY, T. E., BIERREGAARD, R. O., JR., RANKIN, R. M. & SCHUBART, H. R. O. (1983). Ecological dynamics of the tropical forest fragments. In *Tropical Rain Forest Ecology and Managment* (eds. S. L. Sutton, T. C. Whitmore and A. C. Chadwick). Blackwell Scientific Publications, London.

LOVEJOY, T. E., BIERREGAARD, R. O., JR., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., JR., POWELL, A. H., POWELL, G. V. N., SCHUBART, H. R. O. & HAYS, M. B. (1986). Edge and other effects of isolation on Amazonian forest fragments. In *Conservation Biology: the Science of Scarcity and Diversity.* (ed. M. E. Soulé), pp. 257−285. Sinauer, Sunderland.

LOVEJOY, T. E., RANKIN, R. M., BIERREGAARD, R. O., JR., BROWN, K. S., EMMONS, L. H. & VAN DER VOORT, M. E. (1984). Ecosystem decay of Amazon forest fragments. In *Extinctions.* (ed. M. N. Nitecki), pp. 295−325. University of Chicago Press, Chicago.

LOWMAN, M. D. (1992). Herbivory in Australian rain forests, with particular references to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica* **24,** 263−272.

LOWMAN, M. D., MOFFETT, M. & RINKER, H. B. (1993). A new technique for taxonomic and ecological sampling in rain forest canopies. *Selbyana* **14,** 75−79.

LUCKY, A., ERWIN, T. L. & WITMAN, J. D. (2002). Temporal and spatial diversity and distribution of arboreal Carabidae (Coleoptera) in a western Amazonian rain forest. *Biotropica* **34,** 376−386.

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 Archives, Vol. XXXV, Part B (CD Rom), Proceedings of the ISPRS XXth Congress, 12−23 Juli 2004*, Istanbul.

MACARTHUR, R. H. & WILSON, E. O. (1967). *The theory of island biogeography.* Princeton University Press, Princeton.

MAGURRAN, A. E. (1988). *Ecological diversity and its measurement.* Croom Helm, London.

MALCOLM, J. R. (1994). Edge effects in Amazonian forest fragments. *Ecology* **75,** 2438–2445.

MALCOLM, J. R. (1997). Insect biomass in Amazonian forest fragments. In *Canopy Arthropods* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 511–533. Chapman & Hall, London.

MARQUES, M. I., ADIS, J., DA CUNHA, C. N. & DOS SANTOS, G. B. (2001). Arthropod Biodiversity in the Canopy of *Vochysia divergens* (Vochysiaceae), a Forest Dominant in the Brazilian Pantanal. *Studies on Neotropical Fauna and Environment* **36,** 205–210.

MARTINS, M. B. (1989). Invasao de fragmentos florestais por espécies oportunistas de *Drosophila* (Diptera, Drosophilidae). *Acta Amazonica* **19,** 265–271.

MASAKI, S. (1980). Summer diapause. *Annual Review of Entomology* **25,** 1–25.

MAWDSLEY, N. A. & STORK, N. E. (1997). Host-specificity and the effective specialization of tropical canopy beetles. In *Canopy Arthropods.* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 104–130. Chapman & Hall, London.

MAY, R. M. (1975). Patterns of species abundance and diversity. In *Ecology and evolution of communities.* (eds. M. L. Cody and J. M. Diamond), pp. 81–120. Harvard University Press, Cambridge, Mass.

MAY, R. M. (1986). How many species are there? *Nature* **324,** 514–515.

MAY, R. M. (1990). How many species? *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **330,** 293–304.

MCARDLE, B. H. (1990). When are rare species not there? *Oikos* **57,** 276–277.

MCINTOSH, R. P. (1967). An index of diversity and the relation of certain concepts to diversity. *Ecology* **48,** 392–404.

MEMMOT, J., GODFRAY, H. C. J. & BOLTON, B. (1993). Predation and parasitism in a tropical herbivore community. *Ecological Entomology* **18,** 348–352.

MESQUITA, R. C. G., DELAMONICA, P. & LAURANCE, W. F. (1999). Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* **91,** 129–134.

MICHAUD, J. P. (1990). Conditions for the evolution of polyphagy in herbivorous insects. *Oikos* **57,** 278–279.

MIDDELHAUVE, J. & WAGNER, T. (2001). Revision of *Afrocrania* (Coleoptera: Chrysomelidae, Galerucinae). Part I: Species in which the males have head cavities or extended elytral extrusions. *European Journal of Entomology* **98,** 511–531.

MITCHELL, A. W. (1982). *Reaching the Rain Forest Roof.* Leeds Philosophical and Literary Society, Leeds.

MITCHELL, N. (2004). BIOTA East Report No. 1. The exploitation and disturbance history of Kakamega Forest, Western Kenya. In *Bielefelder Ökologische Beiträge. Band 20* (eds. Bärbel Bleher and Helmut Dalitz), pp. 77. Gesellschaft für Forschung und Technologie, Universität Bielefeld.

MOFFETT, M. (1993). *The High Frontier. Exploring the Tropical Rainforest Canopy.* Harvard University Press, Cambridge, MA.

MORISITA, M. (1959). Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)* **3,** 65−80.

MORRIS, M. G. & RISPIN, W. E. (1988). A beetle fauna of Oolitic limestone grassland, and responses of species to conservation management by different cutting regimes. *Biological Conservation* **43,** 87−105.

MORSE, D. R., STORK, N. E. & LAWTON, J. H. (1988). Species number, species abundance and body lenght relationship of arboreal beetles in Bornean lowland rain forest trees. *Ecological Entomology* **13,** 25−37.

MURCIA, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* **10,** 58−62.

MUTANGAH, J. G., MWANGANGI, O. & MWAURA, P. K. (1992). A Vegetation Survey Report. Kakamega Forest. Kenya Indigenous Forest Conservation Programme, National Museums of Kenya, Nairobi.

MYERS, N. (1979). *The sinking ark.* Pergamon Press, Oxford etc.

MYERS, N. (1988). Threatened biotas: "Hot spots" in tropical forests. *The Environmentalist* **8,** 187−208.

MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403,** 853−858.

NEW, T. R., ADIS, J. U., MORAIS, J. W. & GOMES RODRIGUES, J. M. (1991). Notes on phenology and abundance of Psocoptera from primary and secondary dryland forest in central Amazonia, Brazil. *Studies on Neotropical Fauna and Environment* **26,** 243−247.

NIEMELAE, P. & TUOMI, J. (1987). Does the leaf morphology of some plants mimic caterpillar damage? *Oikos* **50,** 256−257.

NOVOTNY, V. & BASSET, Y. (1998). Seasonality of sap-sucking insects (Auchenorryncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rainforest in New Guinea. *Oecologia* **115,** 514−522.

NOVOTNY, V., BASSET, Y. & KITCHING, R. L. (2003). Herbivore assemblages and their food resources. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 40−53. University Press, Cambridge.

NOVOTNY, V., BASSET, Y., MILLER, S. E., DROZD, P. & CIZEK, L. (2002a). Host specialisation of leaf-chewing insects in a New Guinean rain forest. *Journal of Animal Ecology* **71,** 400−412.

NOVOTNY, V., BASSET, Y., MILLER, S. E., WEIBLEN, G. D., BREMER, B., CIZEK, L. & DROZD, P. (2002b). Low host specificity of herbivorous insects in a tropical forest. *Nature* **416,** 841−844.

NOVOTNY, V., BASSET, Y., SAMUELSON, G. A. & MILLER, S. E. (1999). Host use by chrysomelid beetles feeding on *Ficus* (Moraceae) and Euphorbiaceae in New Guinea. In *Advances in Chrysomelidae Biology 1* (ed. M. L. Cox), pp. 343−360. Backhuys, Leyden.

NOYES, J. S. (1989). The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecological Entomology* **14,** 197−207.

ØDEGARD, F. (2003). Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 220−236. University Press, Cambridge.

OYUGI, J. O. (1996). Kakamega Forest is dying. *Bulletin of the EANHS* **26,** 47−49.

OZANNE, C. M. P., HAMBLER, C., FOGGO, A. & SPEIGHT, M. R. (1997). The significance of edge effects in the management of forests for invertebrate biodiversity. In *Canopy Arthropods.* (ed. R. K. Didham), pp. 534−550. Chapman & Hall, London.

PAARMANN, W. (1994). Von der Tötung zum Lebendfang - Entwicklung der Insektizidnebeltechnik. *Allgemeine Forstzeitschrift* **49,** 1457−1459.

PAARMANN, W. & KERCK, K. (1997). Advances in using the canopy fogging technique to collect living arthropods from tree-crowns. In *Canopy Arthropods.* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 53−66. Chapman & Hall, London.

PAARMANN, W. & PAARMANN, D. (1997). Studies on the biology of a canopy-dwelling carabid beetle collected by canopy fogging in the rainforest of Sulawesi (Indonesia). In *Canopy Arthropods.* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 433−441. Chapman & Hall, London.

PAARMANN, W. & STORK, N. E. (1987). Canopy fogging, a method for collecting living insects for investigations of live history strategies. *Journal of natural History* **21,** 563−566.

PALACIOS-VARGAS, J. G. & CASTANO-MENESES, G. (2003). Seasonality and community composition of springtails in Mexican forests. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 159−175. University Press, Cambridge.

PETERSON, A. T. & SLADE, N. A. (1998). Extrapolating inventory results into biodiversity estimates and the importance of stopping rules. *Diversity and Distributions* **4,** 95−105.

PICKETT, S. T. A. & CADENASSO, M. L. (1995). Landscape ecology: spatial heterogeneity in ecological systems. *Science* **269,** 331−334.

PIELOU, E. C. (1969). *An Introduction to Mathematical Ecology.* Wiley, New York.

PIMM, S. L., JONES, H. L. & DIAMOND, J. M. (1988). On the risk of extinction. *The American Naturalist* **132,** 757−785.

PRICE, P. W. (1991). Patterns in communities along latitudinal gradients. In *Plant-animal interactions.* (eds. P. W. Price, Th. M. Lewinsohn, G. W. Fernandes and W. W. Benson), pp. 51−69. Wiley & Sons, New York etc.

PRICE, P. W., BURTON, C. E., GROSS, P., MCPHERON, B. A., THOMPSON, J. N. & WEIS, A. E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11,** 41−65.

PRICE, P. W., DINIZ, I. R., MORAIS, H. C. & MARQUES, S. A. (1995). The abundance of insect herbivore species in the tropics: The high local richness of rare species. *Biotropica* **27,** 468−478.

PSCHORN-WALCHER, H. (1985). Konkurrenz und Mannigfaltigkeit bei Parasitoiden. *Zeitschrift für zoologische Systematik und Evolutionsforschung* **23,** 286−298.

PYLE, R., BENTZIEN, M. & OPLER, P. (1981). Insect conservation. *Annual Review of Entomology* **26,** 233−258.

REICHLE, D. E., GOLDSTEIN, R. A., VAN HOOK, R. I., JR. & DODSON, G. J. (1973). Analysis of insect consumption in a forest canopy. *Ecology* **54,** 1076−1084.

REID, C. A. M. (1995). A cladistic analysis of subfamilial relationships in the Chrysomelidae sensu latu (Chrysomelidae). In *Biology, Phylogeny and Classification of Coleoptera: Papers Celebrating the 80th Birthday of Roy A. Crowson.* (eds. J. Pakaluk and S. A. Slipinski), pp. 559−632. Museum i Instytut Zoologii PAN, Warszawa.

RODGERS, A. (1992). Eastern Africa. In *The Conservation Atlas of Tropical Forests-Africa* (eds. Jeffrey A. Sayer, Caroline S. Harcourt and N. Mark Collins), pp. 143−160. Macmillan Publishers Ltd., United Kingdom.

RODRIGUES, J. J. S., BROWN, K. S. & RUSZCZYK, A. (1993). Resources and conservation of Neotropical butterflies in urban forest fragments. *Biological Conservation* **64,** 3−9.

ROLAND, J. (1993). Large-scale forest fragmentation increases the duration of tent caterpillar outbreaks. *Oecologia* **93,** 25−30.

ROSENBERG, D. M., DANKS, H. V. & LEHMKUHL, D. M. (1986). Importance of insects in environmental impact assessment. *Environmental Management* **10,** 773−783.

ROSSIGNOL-STRICK, M. (1983). African monsoons, an immediate climate response to orbital insolation. *Nature* **304,** 105−134.

ROUBIK, D. W., SAKAI, S. & GATTESCO, F. (2003). Canopy flowers and certainty: loose niches revisited. In *Arthropods in Tropical Forests* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 360−368. University Press, Cambridge.

SACHS, L. (1992). *Angewandte Statistik, 7. Auflage.* Springer, Berlin etc.

SAMWAYS, M. J. (1988). Classical biological control and insect conservation: are they compatible? *Environmental Conservation* **15,** 97−111.

SAMWAYS, M. J. (1990). Insect conservation ethics. *Environmental Conservation* **17,** 7−8.

SANDERS, H. L. (1968). Marine benthic diversity: a comparative study. *American Naturalist* **102,** 243−282.

SAUNDERS, D. A., HOBBS, J. R. & MARGULES, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5,** 18−32.

SCHOENER, T. W. (1982). The controversy over interspecific competition. *American Scientist* **70,** 586−595.

SCHOENER, T. W. (1986). Overview: kinds of ecological communities - ecology becomes pluralistic. In *Community ecology.* (eds. J. M. Diamond and T. J. Case), pp. 467−479. Harper & Row, New York.

SCHÖLLER, M. (1996). Ökologie mitteleuropäischer Blattkäfer, Samenkäfer und Breitrüssler. In *Sonderabdruck aus: Die Blatt- und Samenkäfer von Vorarlberg und Liechtenstein.* (ed. Erster Vorarlberger Coleopterologischer Verein). Selbstverlag, Bürs.

SCHOWALTER, T. D. & GANIO, L. M. (2003). Diel, seasonal and disturbance-induced variation in invertebrate assemblages. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 315−328. University Press, Cambridge.

SCHULZ, A. & WAGNER, T. (2002). Influence of forest type and tree species on canopy ants (Hymenoptera: Formicidae) in Budongo Forest, Uganda. *Oecologia* **133,** 224−232.

SCRIBER, J. M. & SLANSKY, F., JR. (1981). The nutritional ecology of immature insects. *Annual Review of Entomology* **26,** 183−211.

SHAFFER, M. L. (1981). Minimum population sizes for species conservation. *BioScience* **31,** 131−134.

SHANNON, C. E. & WEAVER, W. (1949). *The mathematical theory of communication.* University of Illinois Press, Urbana.

SHREEVE, T. G. & MASON, C. F. (1980). The number of butterfly species in woodland. *Oecologia* **45,** 414−418.

SIMBERLOFF, D. (1979). Rarefaction as a distribution-free method of expressing and estimating diversity. In *Ecological Diversity in Theory and Practice.* (eds. J. F. Grassle, G. P. Patil, W. Smith and C. Taillie), pp. 159−176. International Cooperative Publishing House, Fairland, Md.

SIMON, H.-R. (1996). Die artenreichsten Insekten-Ordnungen. Teil 2: Anzahl rezenter Arten mit Anmerkungen zur ökologischen Signifikanz. *Entomologische Zeitschrift* **106,** 5−29.

SIMPSON, E. H. (1949). Measurement of diversity. *Nature* **163,** 688.

SOUTHWOOD, T. R. E., MORAN, V. C. & KENNEDY, C. E. (1982). The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* **51,** 635−649.

STEHR, F. W. (1987). Immature Insects, Volume 1, pp. 754. Kendall/Hunt Publishing Company, Dubuque, Iowa.

STEHR, F. W. (1991). Immature Insects, Volume 2, pp. 974. Kendall/Hunt Publishing Company, Dubuque, Iowa.

STEIN, R. & SARNTHEIN, M. (1984). Late Neogene events of atmospheric and oceanic circulation offshore Northwest Africa: high resolution record from deep-sea sediments. *Palaeoecology of Africa* **13,** 9−36.

STERCK, F., VAN DER MEER, P. & BONGERS, F. (1992). Herbivory in two rainforest canopies in French Guyana. *Biotropica* **24,** 97−99.

STORK, N. E. (1987a). Arthropod faunal similarity of Bornean rain forest trees. *Ecological Entomology* **12,** 219−226.

STORK, N. E. (1987b). Guild structure of arthropods from Bornean rain forest trees. *Ecological Entomology* **12,** 69−80.

STORK, N. E. (1988). Insect diversity: Facts, fiction and speculation. *Biological Journal of the Linnean Society* **35,** 321−337.

STORK, N. E. (1991). The composition of the arthropod fauna of Bornean lowland rain forest trees. *Journal of tropical Ecology* **7,** 161−180.

STORK, N. E. & BRENDELL, M. J. D. (1990). Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. In *Insects and the rainforest of South East Asia (Wallacea).* (eds. W. J. Knight and J. D. Holloway). Royal entomological Society of London, London.

STORK, N. E. & HAMMOND, P. M. (1997). Sampling arthropods from tree-crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (UK). In *Canopy Arthropods* (eds. N. E. Stork, J. Adis and R. K. Didham), pp. 3−26. Chapman & Hall, London.

STRAUSS, S. (1988). The Chrysomelidae: A useful group for investigating herbivore-herbivore interactions. In *Biology of Chrysomelidae.* (eds. P. H. Jolivet, E. Petitpierre and T. H. Hsiao), pp. 95−105. Kluiver Academic Publishers, Dordrecht, etc.

STRONG, D. R., JR. (1982). Natural variability and the manifold mechanisms of ecological communities. *American Naturalist* **122,** 636−660.

SUTTON, S. L. (2001). Alice grows up: canopy science in transition from Wonderland to Reality. *Plant Ecology* **153,** 13−21.

TABARELLI, M., MANTOVANI, W. & PERES, C. A. (1999). Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* **91,** 119−127.

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.

THOMAS, C. D. (1990). Fewer species. *Nature* **347,** 237.

THOMAS, C. D., THOMAS, J. A. & WARREN, M. S. (1992). Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92,** 563−567.

THOMPSON, L. G., MOSLEY-THOMPSON, E., DAVIS, M. E., HENDERSON, K. A., BRECHER, H. H., ZAGORODNOV, V. S., MASHIOTTA, T. A., LIN, P.-N., MIKHALENKO, V. N., HARDY, D. R. & BEER, J. (2002). Kilimanjaro Ice Core Records: Evidence of Holocene Climate Change in Tropical Africa. *Science* **298,** 589−593.

TOBIN, J. E. (1991). A neotropical rainforest canopy, ant community: some ecological considerations. In *Ant-Plant Interactions* (eds. C. R. Huxley and D. F. Cutler), pp. 536−538. University Press, Oxfort.

TOBIN, J. E. (1994). Ants as primary consumers: diet and abundance in the Formicidae. In *Nourishment and Evolution in Insect Societies.* (eds. J. H. Hunt and C. A. Napela), pp. 279−307. Westview Press, Boulder, CO.

TSINGALIA, T. T. (1988). Animals and the regeneration of an African rainforest tree. PhD thesis, University of California, USA.

TURCHIN, P., TAYLOR, A. D. & REEVE, J. D. (1999). Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* **285,** 1068−1070.

TURNER, I. M. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* **33,** 200−209.

UNEP. (2002). State of the environment and policy retrospective: 1972−2002: Forests. In *Global Environment Outlook (GEO) 3. Past, presence and future perspectives.*, pp. 90−100. Earthscan Publisher Ltd., London; Sterlin, VA.

VAN CAMPO, E., DUPLESSY, J. C. & ROSSIGNOL-STRICK, M. (1982). Climatic conditions deduced from 150-Kyr oxygen isotope-pollen record from the Arabian Sea. *Nature* **296,** 56−59.

VANDERMEER, J. (1982). To be rare is to be chaotic. *Ecology* **63,** 1167−1168.

VIEJO, J. L., DEVIEDMA, M. G. & MARTINEZ, F. (1989). The importance of woodlands in the conservation of butterflies (Lep. Papilionidae and Hesperioidae) in the centre of the Iberian Peninsula. *Biological Conservation* **48,** 101−114.

VILLARD, M.-A. (2002). Habitat fragmentation: major conservation issue or intellectual attractor? *Ecological Applications* **12,** 319−320.

WAGNER, T. (1996). Zusammensetzung der baumbewohnenden Arthropodenfauna in Wäldern Zentralafrikas; mit Anmerkungen zur Nebelmethode und zum Morphotypen-Verfahren. *Mitteilungen des Internationalen Entomologischen Vereins e.V.* **21,** 25−42.

WAGNER, T. (1997). The beetle fauna of different tree species in forests of Rwanda and East Zaire. In *Canopy Arthropods* (eds. Nigel E. Stork, J. Adis and R. K. Didham), pp. 169−183. Chapman & Hall, London.

WAGNER, T. (2000a). Influence of forest type and tree species on canopy-dwelling beetles in Budongo forest, Uganda. *Biotropica* **32,** 502−514.

WAGNER, T. (2000b). Revision of afrotropical *Monolepta* species (Coleoptera, Chrysomelidae, Galerucinae). Part I: Species with red and black coloured elytra, pronotum and head, with description of new species. *Entomologische Zeitschrift* **110,** 226−237.

WAGNER, T. (2001). Seasonal changes in the canopy arthropod fauna in *Rinorea beniensis* in Budongo Forest, Uganda. *Plant Ecology* **153,** 169−178.

WAGNER, T. (2002). Verteilungsmuster von Arthropoden in Wäldern Ostafrikas - Einfluss der Ameisen und Abhängigkeit von Waldstruktur, Saisonalität und Höhenlage. In *Konfliktfeld Biodiversität. Darmstädter interdisziplinäre Beiträge 7.* (eds. M. Hummel, J. Scheffran and H.-R. Simon), pp. 199−218. Agenda Verlag, Münster.

WAGNER, T. (2003). Seasonality of canopy beetles in Uganda. In *Arthropods of Tropical Forests.* (eds. Yves Basset, Vojtech Novotny, Scott E. Miller and Roger L. Kitching), pp. 146−158. University Press, Cambridge.

WAGNER, T. & FREUND, W. (2003). Revision of *Barombiella violacea* (Jacoby, 1894) (Coleoptera: Chrysomelidae, Galerucinae). *Entomologische Zeitschrift* **113,** 258−262.

WAGNER, T. & SCHERZ, X. (2002). *Afrocandezea* gen. nov. from tropical Africa (Coleoptera: Chrysomelidae, Galerucinae). *Entomologische Zeitschrift* **112,** 357−362.

WATANABE, H. & RUAYSONNGNERN, S. (1989). Estimation of arboreal arthropod density in a dry evergreen forest in Northeastern Thailand. *Journal of tropical Ecology* **5,** 151−158.

WEBB, N. R. (1989). Studies on the invertebrate fauna of fragmented heathland in Dorset, UK, and the implications for conservations. *Biological Conservation* **47,** 153−165.

WIENS, J. A. (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological Communities. Conceptual Issues and the Evidence.* (eds. D. R. Strong, D. Simberloff, L. G. Abele and A. Thistle), pp. 439−457. Princeton, New Jersey.

WILLIAMS-LINERA, G. (1990a). Origin and development of forest edge vegetation in Panama. *Biotropica* **22,** 235−241.

WILLIAMS-LINERA, G. (1990b). Vegetation structure and environmental conditions of forest edges in Panama. *Journal of Ecology* **78,** 356−373.

WILLIAMSON, M. H. & LAWTON, J. H. (1991). Fractal geometry of ecological habitats. In *Habitat structure-The physical arrangement of objects in space.* (eds. S. S. Bell, E. D. McCoy and H. R. Mushinsky), pp. 69−86. Chapman & Hall, London.

WILSON, E. O. (1988). Biodiversity. National Academy Press, Washington D.C.

WOLDA, H. (1978). Fluctuations in abundance of tropical insects. *American Naturalist* **112,** 1017−1045.

WOLDA, H. (1979). Abundance and diversity of Homoptera in the canopy of a tropical rainforest. *Ecological Entomology* **4,** 181−190.

WOLDA, H. (1981). Similarity indices, sample size and diversity. *Oecologia* **50,** 296−302.

WOLDA, H. (1988). Insect seasonality: Why? *Annual Review of Ecology and Systematics* **19,** 1−18.

WOLDA, H. (1992a). Seasonal reproductive strategies in some Panamian beetles. *Studies on Neotropical Fauna and Environment* **27,** 91−99.

WOLDA, H. (1992b). Trends in abundance of tropical forest insects. *Oecologia* **89,** 47−52.

WOLDA, H. & DENLINGER, D. L. (1984). Diapause in a large aggregation of a tropical beetle. *Ecological Entomology* **9,** 217−230.

WOODMAN, R. L. & PRICE, P. W. (1992). Differential larval predation by ants can influence willow sawfly community structure. *Ecology* **73,** 1028−1037.

YOUNG, A. & MITCHELL, N. (1994). Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation* **67,** 63−72.

Appendix

Appendix 1: Overview of trees examined. The abbreviations are subsequently used in graphs, tables and figures.

sample site	tree species	tree number	canopy height (m)	canopy density (%)	session I 2001	session II 2002	session III 2002	session IV 2003	Abbreviation
Busambuli	*Teclea nobilis*	T.n. 131	4,5 − 11	70	18.X.	25.I.	27.IX.	16.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 132	4 − 8,5	40	18.X.	25.I.	27.IX.	16.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 133	4 − 8	40	18.X.	25.I.	27.IX.	16.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 134	5 − 10	40	18.X.	25.I.	27.IX.	16.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 135	4 − 7,5	45	19.X.	26.I.	28.IX.	17.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 136	5 − 9	55	19.X.	26.I.	28.IX.	17.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 137	5 − 8	30	19.X.	26.I.	28.IX.	17.I.	**bus**
Busambuli	*Teclea nobilis*	T.n. 138	3 − 9	65	19.X.	26.I.	28.IX.	17.I.	**bus**
Isiukhu	*Teclea nobilis*	T.n. 111	3 − 6,5	40	14.IX.	16.I.	22.IX.	12.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 112	3 − 8	60	14.IX.	16.I.	22.IX.	12.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 113	5 − 8	50	14.IX.	16.I.	22.IX.	13.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 114	4 − 11	40	14.IX.	16.I.	30.IX.	13.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 115	4 − 6	30	15.IX.	16.I.	30.IX.	12.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 116	7 − 12	55	15.IX.	16.I.	22.IX.	12.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 117	4 − 10	45	15.IX.	18.I.	30.IX.	13.I.	**isi**
Isiukhu	*Teclea nobilis*	T.n. 118	3 −8	80	15.IX.	18.I.	30.IX.	13.I.	**isi**
Yala	*Teclea nobilis*	T.n. 121	5,5 − 11	60	16.X.	11.I.	04.X.	14.I.	**yal**
Yala	*Teclea nobilis*	T.n. 122	4 − 8	45	16.X.	11.I.	01.X.	14.I.	**yal**
Yala	*Teclea nobilis*	T.n. 123	6 − 10	65	16.X.	17.I.	04.X.	14.I.	**yal**
Yala	*Teclea nobilis*	T.n. 124	6 − 11	50	16.X.	17.I.	04.X.	14.I.	**yal**
Yala	*Teclea nobilis*	T.n. 125	4 − 7,5	45	17.X.	17.I.	04.X.	15.I.	**yal**
Yala	*Teclea nobilis*	T.n. 126	5 − 9	50	17.X.	17.I.	01.X.	15.I.	**yal**
Yala	*Teclea nobilis*	T.n. 127	4 − 8,5	65	17.X.	17.I.	01.X.	15.I.	**yal**
Yala	*Teclea nobilis*	T.n. 128	4 − 6,5	35	17.X.	17.I.	01.X.	15.I.	**yal**
Colobus	*Teclea nobilis*	T.n. 101	4 − 10	65	12.IX.	7.I.	24.IX.	23.I.	**col**
Colobus	*Teclea nobilis*	T.n. 102	5,5 − 8,5	50	12.IX.	7.I.	24.IX.	23.I.	**col**
Colobus	*Teclea nobilis*	T.n. 103	4,5 − 8,5	65	12.IX.	7.I.	24.IX.	23.I.	**col**
Colobus	*Teclea nobilis*	T.n. 104	7 − 10,5	70	12.IX.	7.I.	24.IX.	23.I.	**col**
Colobus	*Teclea nobilis*	T.n. 105	6 −13	70	13.IX.	8.I.	26.IX.	24.I.	**col**
Colobus	*Teclea nobilis*	T.n. 106	4 − 6,5	55	13.IX.	8.I.	26.IX.	24.I.	**col**
Colobus	*Teclea nobilis*	T.n. 107	7 − 9	50	13.IX.	8.I.	25.IX.	24.I.	**col**
Colobus	*Teclea nobilis*	T.n. 108	6 − 9	70	13.IX.	8.I.	25.IX.	24.I.	**col**
Colobus	*Heinsenia diervilleoides*	H.d. 01	5 − 9	50	18.IX.	22.I.	03.X.	21.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 02	4,5 − 9	45	18.IX.	22.I.	03.X.	21.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 03	5 − 8,5	55	18.IX.	22.I.	24.IX.	20.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 04	3,5 − 6	60	18.IX.	22.I.	02.X.	20.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 05	3,5 − 7	40	19.IX.	23.I.	02.X.	20.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 06	2,5 − 5	50	19.IX.	23.I.	03.X.	20.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 07	3 − 7,5	50	19.IX.	24.I.	03.X.	21.I.	**hein**
Colobus	*Heinsenia diervilleoides*	H.d. 08	3 − 7	40	19.IX.	24.I.	24.IX.	21.I.	**hein**
Kisere	*Heinsenia diervilleoides*	H.d. 11	3,5 − 6,5	50	21.IX.	09.I.	09.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 12	4 − 8	45	21.IX.	09.I.	09.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 13	4 − 7	60	22.IX.	09.I.	08.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 14	4 − 6	55	22.IX.	09.I.	08.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 15	2,5 − 7	85	24.IX.	10.I.	05.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 16	3 − 9	50	24.IX.	10.I.	05.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 17	4 − 7	40	24.IX.	10.I.	05.X.	22.I.	**kis**
Kisere	*Heinsenia diervilleoides*	H.d. 18	4,5 − 6,5	35	24.IX.	10.I.	05.X.	22.I.	**kis**

Appendix 2: Distribution and abundance of Arthropoda collected in X. 2001; other Arthropoda include (in descending order of individuals): Neuropteroidea, Collembola, Blattodea, Mantodea, Pseudoscorpiones, Trichoptera, Dermaptera, Ephemeroptera, Isopoda, Mecoptera, Plecoptera, Isoptera, Chilopoda, Phasmatodea.
Total numbers, Arithmetic mean, *Standard Deviation*, ***Percentage***

X. 2001	Colobus	Isiukhu	Yala	Busambuli	Col. (Hein.)	Kisere	Total
Araneida	**866**	**966**	**422**	**599**	**621**	**546**	**4020**
	108,25	120,75	52,75	74,88	77,63	68,25	83,75
	38,85	*62,03*	*10,44*	*20,50*	*29,66*	*23,71*	*205,11*
	7,09	***11,51***	***4,11***	***4,76***	***9,09***	***6,61***	***6,87***
Acari	**830**	**531**	**234**	**580**	**260**	**453**	**2888**
	103,75	66,38	29,25	72,50	32,50	56,63	60,17
	100,69	*95,00*	*7,50*	*37,31*	*20,19*	*44,63*	*221,24*
	6,80	***6,33***	***2,28***	***4,61***	***3,80***	***5,49***	***4,93***
Ensifera	**533**	**166**	**114**	**150**	**157**	**178**	**1298**
	66,63	20,75	14,25	18,75	19,63	22,25	27,04
	34,10	*15,89*	*12,59*	*11,16*	*10,72*	*9,59*	*156,64*
	4,37	***1,98***	***1,11***	***1,19***	***2,30***	***2,16***	***2,22***
Psocoptera	**352**	**71**	**296**	**191**	**227**	**307**	**1444**
	44,00	8,88	37,00	23,88	28,38	38,38	30,08
	20,49	*7,22*	*10,41*	*14,29*	*22,68*	*30,86*	*101,29*
	2,88	***0,85***	***2,88***	***1,52***	***3,32***	***3,72***	***2,47***
Thysanoptera	**1116**	**596**	**591**	**1097**	**735**	**839**	**4974**
	139,50	74,50	73,88	137,13	91,88	104,88	103,63
	85,79	*113,35*	*25,28*	*47,86*	*47,35*	*49,61*	*234,12*
	9,14	***7,10***	***5,76***	***8,72***	***10,76***	***10,16***	***8,50***
Heteroptera	**417**	**352**	**359**	**437**	**226**	**296**	**2087**
	52,13	44,00	44,88	54,63	28,25	37,00	43,48
	32,84	*27,38*	*14,60*	*18,60*	*15,93*	*12,92*	*77,98*
	3,42	***4,19***	***3,50***	***3,47***	***3,31***	***3,58***	***3,57***
Homoptera	**1144**	**688**	**1007**	**2258**	**1083**	**1478**	**7658**
	143,00	86,00	125,88	282,25	135,38	184,75	159,54
	75,87	*55,21*	*48,19*	*187,50*	*57,34*	*83,48*	*543,67*
	9,37	***8,20***	***9,81***	***17,95***	***15,85***	***17,90***	***13,08***
Coleoptera	**1545**	**748**	**1506**	**1418**	**513**	**537**	**6267**
	193,13	93,50	188,25	177,25	64,13	67,13	130,56
	105,60	*68,52*	*79,02*	*60,82*	*16,02*	*27,58*	*496,17*
	12,66	***8,91***	***14,67***	***11,27***	***7,51***	***6,50***	***10,71***
Coleoptera (Larvae)	**129**	**79**	**48**	**122**	**47**	**47**	**472**
	16,13	9,88	6,00	15,25	5,88	5,88	9,83
	6,73	*8,11*	*11,07*	*12,50*	*2,70*	*3,83*	*38,36*
	1,06	***0,94***	***0,47***	***0,97***	***0,69***	***0,57***	***0,81***
Hymenoptera (parasitoid)	**1658**	**783**	**1285**	**1490**	**740**	**749**	**6705**
	207,25	97,88	160,63	186,25	92,50	93,63	139,69
	135,08	*82,09*	*47,17*	*68,72*	*24,57*	*68,66*	*412,10*
	13,58	***9,33***	***12,51***	***11,85***	***10,83***	***9,07***	***11,45***
Symphyta (Larvae)	**45**	**420**	**0**	**179**	**0**	**129**	**773**
	5,63	52,50	0,00	22,38	0,00	16,13	16,10
	5,40	*55,06*	*0,00*	*17,78*	*0,00*	*10,27*	*159,70*
	0,37	***5,00***	***0,00***	***1,42***	***0,00***	***1,56***	***1,32***
Formicidae	**1102**	**787**	**1798**	**1308**	**734**	**1010**	**6739**
	137,75	98,38	224,75	163,50	91,75	126,25	140,40
	101,23	*58,15*	*296,06*	*109,54*	*55,23*	*85,82*	*391,73*
	9,03	***9,38***	***17,51***	***10,40***	***10,74***	***12,23***	***11,51***
Formicidae (Larvae)	**0**	**0**	**0**	**0**	**0**	**0**	**0**
	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	0,00	*0,00*	*0,00*	*0,00*	*0,00*	*0,00*	*0,00*
	0,00	***0,00***	***0,00***	***0,00***	***0,00***	***0,00***	***0,00***
Lepidoptera	**9**	**14**	**0**	**9**	**5**	**4**	**41**
	1,13	1,75	0,00	1,13	0,63	0,50	0,85
	1,89	*1,58*	*0,00*	*1,73*	*1,19*	*0,76*	*4,88*
	0,07	***0,17***	***0,00***	***0,07***	***0,07***	***0,05***	***0,07***
Lepidoptera (Larvae)	**212**	**297**	**447**	**1049**	**470**	**482**	**2957**
	26,50	37,13	55,88	131,13	58,75	60,25	61,60
	8,55	*11,48*	*34,49*	*130,26*	*16,33*	*14,49*	*293,01*
	1,74	***3,54***	***4,35***	***8,34***	***6,88***	***5,84***	***5,05***
Diptera	**1994**	**1662**	**2002**	**1375**	**879**	**1006**	**8918**
	249,25	207,75	250,25	171,88	109,88	125,75	185,79
	148,53	*186,61*	*94,07*	*103,89*	*63,46*	*93,31*	*483,00*
	16,33	***19,80***	***19,50***	***10,93***	***12,86***	***12,18***	***15,23***
Diptera (Larvae)	**91**	**111**	**29**	**78**	**49**	**113**	**471**
	11,38	13,88	3,63	9,75	6,13	14,13	9,81
	12,06	*14,71*	*7,15*	*5,06*	*2,36*	*13,61*	*33,83*
	0,75	***1,32***	***0,28***	***0,62***	***0,72***	***1,37***	***0,80***
Arthropoda (others)	**165**	**121**	**131**	**239**	**88**	**84**	**828**
	20,63	15,13	16,38	29,88	11,00	10,50	17,25
	12,73	*16,66*	*9,47*	*23,69*	*6,46*	*4,96*	*57,77*
	1,35	***1,44***	***1,28***	***1,90***	***1,29***	***1,02***	***1,41***
Total	**12208**	**8392**	**10269**	**12579**	**6834**	**8258**	**58540**
	1526,00	1049,00	1283,63	1572,38	854,25	1032,25	1219,58
	670,64	*734,91*	*442,07*	*472,05*	*283,29*	*466,12*	*570,56*

Appendix 3: Distribution and abundance of Arthropoda collected in I. 2002; for details see Appendix 2.

I. 2002	Colobus	Isiukhu	Yala	Busambuli	Col. (Hein.)	Kisere	Total
Araneida	**255**	**373**	**277**	**253**	**395**	**366**	**1919**
	31,88	46,63	34,63	31,63	49,38	45,75	39,98
	9,51	*13,42*	*19,91*	*9,77*	*17,43*	*14,66*	*15,71*
	3,73	***5,02***	***2,86***	***4,67***	***4,55***	***3,13***	***3,86***
Acari	**149**	**359**	**172**	**205**	**200**	**259**	**1344**
	18,63	44,88	21,50	25,63	25,00	32,38	28,00
	11,10	*25,98*	*9,91*	*10,25*	*14,76*	*11,56*	*16,67*
	2,18	***4,83***	***1,78***	***3,78***	***2,30***	***2,21***	***2,70***
Ensifera	**36**	**39**	**49**	**43**	**90**	**58**	**315**
	4,50	4,88	6,13	5,38	11,25	7,25	6,56
	3,82	*3,72*	*4,49*	*3,02*	*8,50*	*4,92*	*5,32*
	0,53	***0,53***	***0,51***	***0,79***	***1,04***	***0,50***	***0,63***
Psocoptera	**1096**	**433**	**844**	**237**	**1506**	**1080**	**5196**
	137,00	54,13	105,50	29,63	188,25	135,00	108,25
	77,03	*29,07*	*77,49*	*8,70*	*49,81*	*63,12*	*76,04*
	16,02	***5,83***	***8,72***	***4,37***	***17,33***	***9,23***	***10,44***
Thysanoptera	**1013**	**1029**	**1077**	**922**	**831**	**1215**	**6087**
	126,63	128,63	134,63	115,25	103,88	151,88	126,81
	50,42	*39,90*	*141,67*	*76,23*	*39,60*	*80,86*	*76,86*
	14,80	***13,85***	***11,13***	***17,00***	***9,56***	***10,38***	***12,23***
Heteroptera	**222**	**275**	**330**	**245**	**463**	**410**	**1945**
	27,75	34,38	41,25	30,63	57,88	51,25	40,52
	14,68	*11,41*	*19,26*	*12,02*	*27,46*	*18,25*	*20,30*
	3,24	***3,70***	***3,41***	***4,52***	***5,33***	***3,50***	***3,91***
Homoptera	**674**	**378**	**706**	**368**	**797**	**977**	**3900**
	84,25	47,25	88,25	46,00	99,63	122,13	81,25
	36,02	*25,84*	*66,73*	*37,63*	*31,46*	*77,81*	*54,55*
	9,85	***5,09***	***7,30***	***6,79***	***9,17***	***8,35***	***7,84***
Coleoptera	**596**	**906**	**1274**	**848**	**742**	**581**	**4947**
	74,50	113,25	159,25	106,00	92,75	72,63	103,06
	24,73	*95,78*	*55,00*	*40,16*	*46,88*	*15,82*	*58,17*
	8,71	***12,20***	***13,17***	***15,64***	***8,54***	***4,96***	***9,94***
Coleoptera (Larvae)	**10**	**12**	**26**	**56**	**12**	**12**	**128**
	1,25	1,50	3,25	7,00	1,50	1,50	2,67
	0,71	*1,41*	*1,58*	*4,24*	*2,67*	*0,93*	*2,99*
	0,15	***0,16***	***0,27***	***1,03***	***0,14***	***0,10***	***0,26***
Hymenoptera (parasitoid)	**1392**	**1875**	**2446**	**927**	**734**	**1108**	**8482**
	174,00	234,38	305,75	115,88	91,75	138,50	176,71
	60,59	*141,94*	*214,27*	*67,91*	*47,31*	*40,77*	*131,00*
	20,34	***25,25***	***25,28***	***17,10***	***8,45***	***9,47***	***17,05***
Symphyta (Larvae)	**0**	**8**	**0**	**0**	**0**	**0**	**8**
	0,00	1,00	0,00	0,00	0,00	0,00	0,17
	0,00	*1,77*	*0,00*	*0,00*	*0,00*	*0,00*	*0,78*
	0,00	***0,11***	***0,00***	***0,00***	***0,00***	***0,00***	***0,02***
Formicidae	**633**	**567**	**1279**	**506**	**1414**	**3652**	**8051**
	79,13	70,88	159,88	63,25	176,75	456,50	167,73
	92,11	*61,53*	*158,95*	*29,59*	*137,32*	*862,34*	*371,88*
	9,25	***7,63***	***13,22***	***9,33***	***16,28***	***31,21***	***16,18***
Formicidae (Larvae)	**0,00**	**1**	**0**	**0**	**0**	**800**	**801**
	0,00	0,13	0,00	0,00	0,00	100,00	16,69
	0,00	*0,35*	*0,00*	*0,00*	*0,00*	*282,84*	*115,47*
	0,00	***0,01***	***0,00***	***0,00***	***0,00***	***6,84***	***1,61***
Lepidoptera	**4**	**5**	**13**	**6**	**6**	**5**	**39**
	0,50	0,63	1,63	0,75	0,75	0,63	0,81
	0,76	*1,41*	*1,19*	*1,04*	*0,89*	*0,74*	*1,05*
	0,06	***0,07***	***0,13***	***0,11***	***0,07***	***0,04***	***0,08***
Lepidoptera (Larvae)	**115**	**282**	**241**	**302**	**260**	**226**	**1426**
	14,38	35,25	30,13	37,75	32,50	28,25	29,71
	7,65	*20,56*	*14,26*	*17,93*	*15,48*	*5,34*	*15,74*
	1,68	***3,80***	***2,49***	***5,57***	***2,99***	***1,93***	***2,87***
Diptera	**458**	**790**	**748**	**409**	**987**	**631**	**4023**
	57,25	98,75	93,50	51,13	123,38	78,88	83,81
	23,13	*72,47*	*71,96*	*28,95*	*88,47*	*31,73*	*60,83*
	6,69	***10,64***	***7,73***	***7,54***	***11,36***	***5,39***	***8,08***
Diptera (Larvae)	**60**	**11**	**35**	**15**	**142**	**10**	**273**
	7,50	1,38	4,38	1,88	17,75	1,25	5,69
	10,39	*2,50*	*7,89*	*5,30*	*24,91*	*1,49*	*12,56*
	0,88	***0,15***	***0,36***	***0,28***	***1,63***	***0,09***	***0,55***
Arthropoda (others)	**130**	**84**	**159**	**80**	**109**	**313**	**875**
	16,25	10,50	19,88	10,00	13,63	39,13	18,23
	13,29	*6,00*	*10,36*	*3,59*	*7,11*	*24,93*	*15,82*
	1,90	***1,13***	***1,64***	***1,48***	***1,25***	***2,67***	***1,76***
Total	**6843**	**7427**	**9676**	**5422**	**8688**	**11703**	**49759**
	855,38	928,38	1209,50	677,75	1086,00	1462,88	1036,65
	266,32	*383,55*	*665,85*	*209,73*	*182,20*	*1168,75*	*615,94*

Appendix 4: Distribution and abundance of Arthropoda collected in X. 2002; for details see Appendix 2.

X. 2002	Colobus	Isiukhu	Yala	Busambuli	Col. (Hein.)	Kisere	Total
Araneida	492	642	708	564	718	469	3593
	61,50	80,25	88,50	70,50	89,75	58,63	74,85
	26,76	46,23	23,46	28,26	40,84	29,96	34,07
	5,84	4,16	4,19	4,54	6,10	4,90	4,82
Acari	452	2315	468	757	226	189	4407
	56,50	289,38	58,50	94,63	28,25	23,63	91,81
	22,70	209,93	38,87	64,24	11,71	13,51	126,70
	5,37	15,01	2,77	6,10	1,92	1,98	5,92
Ensifera	133	70	104	102	109	86	604
	16,63	8,75	13,00	12,75	13,63	10,75	12,58
	9,59	7,05	8,91	9,85	9,59	6,67	8,59
	1,58	0,45	0,62	0,82	0,93	0,90	0,81
Psocoptera	723	1456	1006	1772	759	801	6517
	90,38	182,00	125,75	221,50	94,88	100,13	135,77
	18,49	151,97	55,91	111,25	37,27	75,68	96,66
	8,58	9,44	5,95	14,28	6,45	8,38	8,75
Thysanoptera	906	1178	1459	935	1119	799	6396
	113,25	147,25	182,38	116,88	139,88	99,88	133,25
	42,89	110,85	74,63	65,96	52,26	60,12	72,68
	10,75	7,64	8,63	7,53	9,51	8,35	8,59
Heteroptera	205	702	493	389	344	267	2400
	25,63	87,75	61,63	48,63	43,00	33,38	50,00
	10,10	96,46	16,70	21,32	25,42	21,84	45,82
	2,43	4,55	2,92	3,13	2,92	2,79	3,22
Homoptera	650	1363	3383	556	1519	944	8415
	81,25	170,38	422,88	69,50	189,88	118,00	175,31
	35,20	118,54	240,78	50,89	102,67	61,26	166,94
	7,72	8,84	20,02	4,48	12,91	9,87	11,30
Coleoptera	651	912	1866	1552	589	626	6196
	81,38	114,00	233,25	194,00	73,63	78,25	129,08
	27,10	89,75	78,50	81,73	24,25	38,61	86,52
	7,73	5,91	11,04	12,50	5,01	6,55	8,32
Coleoptera (Larvae)	39	55	76	48	48	28	294
	4,88	6,88	9,50	6,00	6,00	3,50	6,13
	2,53	4,19	4,81	4,18	3,55	2,62	4,00
	0,46	0,36	0,45	0,39	0,41	0,29	0,39
Hymenoptera (parasitoid)	1311	1765	2049	1516	1220	711	8572
	163,88	220,63	256,13	189,50	152,50	88,88	178,58
	58,50	244,31	98,81	111,22	37,13	45,15	126,77
	15,56	11,44	12,12	12,21	10,37	7,43	11,51
Symphyta (Larvae)	16	830	84	389	26	79	1424
	2,00	103,75	10,50	48,63	3,25	9,88	29,67
	2,27	144,47	8,82	28,40	1,91	6,51	67,98
	0,19	5,38	0,50	3,13	0,22	0,83	1,91
Formicidae	552	1245	1832	1343	1799	2199	8970
	69,00	155,63	229,00	167,88	224,88	274,88	186,88
	57,18	137,51	197,20	191,12	220,02	154,51	172,51
	6,55	8,07	10,84	10,82	15,29	22,99	12,04
Formicidae (Larvae)	0,00	14	6	73	184	107	384
	0,00	1,75	0,75	9,13	23,00	13,38	8,00
	0,00	4,95	2,12	25,81	61,48	33,90	30,13
	0,00	0,09	0,04	0,59	1,56	1,12	0,52
Lepidoptera	11	48	18	47	6	4	134
	1,38	6,00	2,25	5,88	0,75	0,50	2,79
	1,51	9,20	1,39	6,15	0,89	1,07	4,95
	0,13	0,31	0,11	0,38	0,05	0,04	0,18
Lepidoptera (Larvae)	211	339	457	797	752	795	3351
	26,38	42,38	57,13	99,63	94,00	99,38	69,81
	14,29	39,89	12,05	61,05	24,67	26,22	43,74
	2,50	2,20	2,70	6,42	6,39	8,31	4,50
Diptera	1935	2248	2635	1315	2138	1338	11609
	241,88	281,00	329,38	164,38	267,25	167,25	241,85
	104,13	377,85	99,84	91,04	94,05	84,47	177,82
	22,97	14,58	15,59	10,59	18,17	13,99	15,58
Diptera (Larvae)	38	16	73	11	51	49	238
	4,75	2,00	9,13	1,38	6,38	6,13	4,96
	7,48	2,27	6,94	3,16	4,27	4,49	5,54
	0,45	0,10	0,43	0,09	0,43	0,51	0,32
Arthropoda (others)	99	225	185	247	159	73	988
	12,38	28,13	23,13	30,88	19,88	9,13	20,58
	5,93	26,94	7,55	9,63	9,17	5,44	14,67
	1,18	1,46	1,09	1,99	1,35	0,76	1,33
Total	8424	15423	16902	12413	11766	9564	74492
	1053,00	1927,88	2112,75	1551,63	1470,75	1195,50	1551,92
	232,30	1471,15	436,68	557,68	465,27	526,95	788,29

Appendix 5: Distribution and abundance of Arthropoda collected in I. 2003; for details see Appendix 2.

I. 2003	Colobus	Isiukhu	Yala	Busambuli	Col. (Hein.)	Kisere	Total
Araneida	423	930	729	848	718	730	4378
	52,88	116,25	91,13	106,00	89,75	91,25	91,21
	23,22	45,65	26,66	43,41	24,21	38,41	38,46
	7,83	8,42	8,62	5,85	8,31	5,64	7,18
Acari	97	439	87	390	208	268	1489
	12,13	54,88	10,88	48,75	26,00	33,50	31,02
	5,54	26,62	6,53	21,79	17,51	20,33	24,08
	1,79	3,97	1,03	2,69	2,41	2,07	2,44
Ensifera	123	40	73	94	100	47	477
	15,38	5,00	9,13	11,75	12,50	5,88	9,94
	8,26	3,82	5,00	7,31	7,82	4,02	7,02
	2,28	0,36	0,86	0,65	1,16	0,36	0,78
Psocoptera	58	532	321	872	133	629	2545
	7,25	66,50	40,13	109,00	16,63	78,63	53,02
	2,92	20,52	10,67	49,99	7,35	54,45	46,79
	1,07	4,82	3,80	6,02	1,54	4,86	4,17
Thysanoptera	428	998	619	1313	483	495	4336
	53,50	124,75	77,38	164,13	60,38	61,88	90,33
	25,99	50,51	31,31	89,92	29,75	31,94	61,59
	7,92	9,04	7,32	9,06	5,59	3,82	7,11
Heteroptera	202	404	306	589	348	616	2465
	25,25	50,50	38,25	73,63	43,50	77,00	51,35
	12,21	19,65	9,59	42,72	25,65	33,18	31,29
	3,74	3,66	3,62	4,06	4,03	4,76	4,04
Homoptera	545	585	557	1606	896	2398	6587
	68,13	73,13	69,63	200,75	112,00	299,75	137,23
	50,44	60,19	43,06	377,95	63,37	250,24	199,94
	10,08	5,30	6,59	11,08	10,38	18,52	10,80
Coleoptera	582	827	1385	1761	536	636	5727
	72,75	103,38	173,13	220,13	67,00	79,50	119,31
	33,77	38,28	64,08	98,50	16,54	26,49	77,21
	10,77	7,49	16,38	12,15	6,21	4,91	9,39
Coleoptera (Larvae)	22	59	31	74	16	17	219
	2,75	7,38	3,88	9,25	2,00	2,13	4,56
	2,25	4,10	3,52	6,14	2,00	2,75	4,51
	0,41	0,53	0,37	0,51	0,19	0,13	0,36
Hymenoptera (parasitoid)	912	1471	1054	2211	763	827	7238
	114,00	183,88	131,75	276,38	95,38	103,38	150,79
	37,96	135,96	60,42	171,54	47,48	31,32	111,56
	16,87	13,32	12,46	15,25	8,84	6,39	11,87
Symphyta (Larvae)	4	0	1	4	1	0	10
	0,50	0,00	0,13	0,50	0,13	0,00	0,21
	0,76	0,00	0,35	0,54	0,35	0,00	0,46
	0,07	0,00	0,01	0,03	0,01	0,00	0,02
Formicidae	400	1391	1118	1466	2241	3679	10295
	50,00	173,88	139,75	183,25	280,13	459,88	214,48
	45,75	172,57	72,64	86,15	243,13	410,39	239,81
	7,40	12,59	13,22	10,11	25,95	28,41	16,88
Formicidae (Larvae)	2,00	159	11	11	316	464	963
	0,25	19,88	1,38	1,38	39,50	58,00	20,06
	0,71	56,22	1,77	3,89	111,72	154,20	79,80
	0,04	1,44	0,13	0,08	3,66	3,58	1,58
Lepidoptera	5	24	6	17	3	11	66
	0,63	3,00	0,75	2,13	0,38	1,38	1,38
	0,74	4,66	1,17	1,96	0,52	1,41	2,30
	0,09	0,22	0,07	0,12	0,03	0,08	0,11
Lepidoptera (Larvae)	110	679	390	991	630	635	3435
	13,75	84,88	48,75	123,88	78,75	79,38	71,56
	6,99	25,50	17,94	45,09	29,36	15,65	42,34
	2,04	6,15	4,61	6,84	7,30	4,90	5,63
Diptera	1417	2368	1649	2015	1121	1336	9906
	177,13	296,00	206,13	251,88	140,13	167,00	206,38
	76,31	261,09	95,00	152,20	53,49	72,19	141,04
	26,22	21,44	19,50	13,90	12,98	10,32	16,24
Diptera (Larvae)	5	7	3	10	15	5	45
	0,63	0,88	0,38	1,25	1,88	0,63	0,94
	0,92	1,36	0,52	1,04	2,70	0,74	1,42
	0,09	0,06	0,04	0,07	0,17	0,04	0,07
Arthropoda (others)	70	132	116	224	108	156	806
	8,75	16,50	14,50	28,00	13,50	19,50	16,79
	4,89	7,56	7,93	11,35	4,69	9,21	9,64
	1,30	1,20	1,37	1,55	1,25	1,20	1,32
Total	5405	11045	8456	14496	8636	12949	60987
	675,63	1380,63	1057,00	1812,00	1079,50	1618,63	1270,56
	186,10	616,95	302,86	837,32	531,05	575,77	646,61

Appendix 6: Individuals and morphotypes of collected beetle taxa in systematic order. Each column represents the results of one collecting unit (eight conspecific trees).

Taxa	Rain season X. 2001														Dry season I. 2002													
	bus		isi		yal		col		hein		kis		Sum		bus		isi		yal		col		hein		kis		Sum	
	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.	n	sp.
Larvae	129	-	79	-	48	-	122	-	47	-	47	-	**472**	-	10	-	12	-	26	-	56	-	12	-	12	-	**128**	-
Adephaga																												
Carabidae	34	11	29	10	21	8	38	11	12	5	19	6	**153**	**20**	12	5	17	4	14	7	5	2	9	5	15	3	**72**	**14**
Staphyliniformia																												
Histeridae	1	1	2	2	1	1	-	-	-	-	-	-	**4**	**4**	2	2	2	1	4	3	-	-	2	2	-	-	**10**	**7**
Leiodidae	-	-	1	1	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Pselaphidae	14	4	22	5	9	6	14	4	25	4	10	3	**94**	**10**	2	1	12	3	10	3	1	1	-	-	1	1	**26**	**7**
Ptiliidae	2	1	4	1	7	2	6	2	3	3	3	2	**25**	**3**	1	1	1	-	1	1	-	-	-	-	3	2	**5**	**3**
Scaphidiidae	202	4	58	5	343	5	82	5	50	6	17	4	**752**	**7**	21	2	21	3	57	5	35	4	18	3	7	2	**159**	**5**
Scydmaenidae	38	3	5	3	48	2	21	2	13	2	13	2	**138**	**3**	13	3	10	2	24	3	2	2	6	2	1	1	**56**	**4**
Staphylinidae	306	34	97	27	269	42	170	44	128	34	119	29	**1089**	**85**	208	20	84	22	161	23	43	21	66	20	124	19	**686**	**56**
Elateriformia																												
Buprestidae	1	1	1	1	4	1	2	1	1	1	2	2	**11**	**2**	3	1	-	-	2	1	2	2	6	2	2	1	**15**	**5**
Cantharidae	9	3	5	3	4	3	27	4	8	1	2	1	**55**	**5**	1	1	-	-	1	1	1	1	-	-	-	-	**3**	**2**
Clambidae	-	-	2	2	1	1	4	3	-	-	-	-	**7**	**3**	-	-	-	-	2	1	1	1	1	1	2	1	**6**	**1**
Drilidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Elateridae	4	2	21	1	8	1	7	2	1	1	-	-	**41**	**3**	8	2	1	1	2	2	5	3	2	2	6	4	**24**	**7**
Eucinetidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**
Lampyridae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**
Lycidae	1	1	5	3	1	1	3	3	-	-	-	-	**10**	**7**	3	1	2	2	3	2	3	2	-	-	1	1	**12**	**4**
Ptilodactylidae	2	1	-	-	-	-	1	1	-	-	-	-	**3**	**3**	-	-	1	1	-	-	-	-	-	-	-	-	**1**	**1**
Scirtidae	1	1	-	-	-	-	2	2	-	-	-	-	**3**	**3**	-	-	2	1	-	-	-	-	-	-	-	-	**2**	**2**
Throscidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	-	-	-	-	-	-	1	1	**1**	**1**
Scarabaeiformia																												
Scarabaeidae	-	-	-	-	1	1	-	-	1	1	1	1	**3**	**2**	1	1	-	-	-	-	-	-	1	1	-	-	**2**	**1**
Bostrichiformia																												
Anobiidae	15	3	-	-	14	4	12	3	1	1	-	-	**42**	**6**	16	6	1	1	13	3	2	2	1	1	-	-	**33**	**6**
Dermestidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Cucujiformia/Cleroidea																												
Cleridae	3	2	1	1	1	1	9	3	-	-	-	-	**14**	**5**	2	2	2	2	1	1	3	1	-	-	-	-	**8**	**4**
Melyridae	3	3	-	-	4	4	8	2	2	1	1	1	**18**	**8**	-	-	1	1	3	3	-	-	-	-	-	-	**4**	**4**
Trogossitidae	4	2	-	-	1	1	2	2	-	-	-	-	**7**	**3**	1	1	2	1	6	2	1	1	-	-	2	1	**12**	**4**
Cucujiformia/Tenebrionoidea																												
Aderidae	3	3	19	9	12	9	20	11	1	1	-	-	**55**	**18**	8	3	4	4	36	8	1	1	1	1	1	1	**51**	**11**
Alleculidae	17	2	18	2	-	-	1	1	-	-	-	-	**36**	**2**	1	1	1	1	-	-	-	-	-	-	-	-	**2**	**1**
Anthicidae	-	-	-	-	-	-	-	-	-	-	1	1	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Ciidae	-	-	-	-	2	1	1	1	-	-	2	2	**5**	**4**	4	4	-	-	2	2	-	-	5	3	2	2	**13**	**11**
Colydiidae	1	1	2	1	2	2	4	1	4	2	1	1	**14**	**6**	-	-	-	-	1	1	4	4	3	1	1	1	**9**	**4**
Lagriidae	3	2	2	1	5	4	6	6	5	4	2	2	**23**	**10**	4	3	2	2	2	1	1	1	-	-	1	1	**10**	**6**
Meloidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**
Mordellidae	2	2	2	1	1	1	6	4	-	-	-	-	**11**	**5**	1	1	2	2	1	1	2	1	-	-	-	-	**6**	**3**
Mycetophagidae	8	2	-	-	4	2	-	-	2	2	-	-	**14**	**4**	12	3	1	1	9	2	1	1	-	-	10	1	**33**	**4**
Rhipiphoridae	-	-	1	1	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	-	-	1	1	2	1	-	-	**3**	**1**
Salpingidae	21	2	16	2	20	2	26	2	4	2	2	1	**89**	**2**	16	2	5	1	22	2	4	1	4	1	-	-	**51**	**2**
Scraptiidae	14	6	10	2	11	7	11	2	-	-	1	1	**47**	**9**	1	1	2	2	3	3	1	1	-	-	2	2	**9**	**5**
Tenebrionidae	21	4	3	3	15	8	5	4	4	2	1	1	**49**	**15**	9	4	3	2	6	4	-	-	3	1	1	1	**22**	**6**
Cucujiformia/Cucujoidea																												
Biphyllidae	9	2	7	1	21	3	37	4	9	3	2	2	**85**	**6**	13	2	12	3	7	4	9	4	5	3	13	1	**59**	**5**
Cerylonidae	-	-	-	-	-	-	-	-	2	2	-	-	**2**	**2**	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**
Coccinellidae	26	10	6	3	10	7	40	18	10	8	3	3	**95**	**28**	13	5	22	13	39	11	60	8	12	7	15	6	**161**	**26**
Corylophidae	329	14	124	14	352	14	140	14	44	10	75	10	**1064**	**20**	278	13	304	15	329	17	35	11	40	10	87	11	**1073**	**18**
Cryptophagidae	8	2	4	1	2	1	3	2	8	1	1	1	**26**	**2**	-	-	6	1	1	1	1	1	-	-	1	1	**9**	**1**
Cucujidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Endomychidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Erotylidae	-	-	-	-	3	1	2	1	-	-	1	1	**6**	**1**	-	-	1	1	1	1	3	2	-	-	-	-	**5**	**3**
Kateretidae	5	1	2	1	1	1	14	2	1	1	-	-	**23**	**3**	1	1	2	1	-	-	1	1	1	1	-	-	**5**	**3**
Laemophloeidae	7	3	1	1	8	2	1	1	3	3	-	-	**20**	**6**	9	3	1	1	8	2	6	3	-	-	-	-	**24**	**6**
Languriidae	3	2	1	1	-	-	2	2	-	-	-	-	**6**	**4**	1	1	1	1	1	1	-	-	6	2	3	1	**12**	**3**
Latridiidae	10	4	11	2	4	3	12	4	1	1	2	1	**40**	**7**	5	4	2	2	3	2	-	-	-	-	3	3	**13**	**6**
Nitidulidae	1	1	-	-	2	2	7	4	4	3	-	-	**14**	**6**	3	2	4	3	1	1	-	-	2	1	-	-	**10**	**5**
Phalacridae	17	7	9	1	12	5	42	8	5	3	5	2	**90**	**12**	13	6	14	5	11	6	14	4	4	2	12	5	**68**	**10**
Propalticidae	-	-	-	-	-	-	1	1	-	-	-	-	**1**	**1**	-	-	-	-	11	2	-	-	-	-	-	-	**11**	**2**
Rhizophagidae	-	-	-	-	-	-	-	-	1	1	-	-	**1**	**1**	-	-	1	1	-	-	-	-	-	-	-	-	**1**	**1**
Silvanidae	-	-	-	-	1	1	1	1	-	-	-	-	**1**	**1**	-	-	-	-	1	1	1	1	-	-	-	-	**1**	**1**
Sphindidae	-	-	2	1	1	1	2	1	4	2	-	-	**9**	**3**	-	-	9	1	-	-	-	-	-	-	-	-	**9**	**1**
Cucujiformia/Chrysomeloidea																												
Cerambycidae	6	4	1	1	11	3	3	3	1	1	1	1	**23**	**8**	5	4	5	4	1	1	1	1	1	1	-	-	**13**	**9**
Alticinae	49	12	55	18	81	17	85	18	31	6	18	8	**319**	**36**	72	11	80	15	177	18	91	13	97	9	55	11	**572**	**27**
Bruchinae	-	-	-	-	-	-	3	2	-	-	-	-	**3**	**2**	-	-	-	-	3	2	4	3	3	2	1	1	**12**	**5**
Cassidinae	6	2	1	1	2	2	-	-	-	-	-	-	**9**	**4**	2	1	1	1	1	1	-	-	-	-	-	-	**3**	**2**
Chrysomelinae	-	-	1	1	-	-	-	-	-	-	-	-	**1**	**1**	-	-	1	1	1	1	-	-	-	-	-	-	**1**	**1**
Criocerinae	-	-	-	-	-	-	1	1	1	1	-	-	**2**	**1**	-	-	-	-	1	1	-	-	-	-	1	1	**2**	**1**
Cryptocephalinae	-	-	-	-	-	-	-	-	-	-	1	1	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Eumolpinae	15	8	58	9	14	8	32	10	2	2	7	5	**128**	**18**	12	7	15	6	11	7	7	6	1	1	7	5	**53**	**18**
Galerucinae	15	10	14	6	8	7	9	7	3	3	3	3	**52**	**21**	22	4	5	5	31	9	3	3	1	1	2	1	**64**	**15**
Hispinae	-	-	1	1	1	1	2	2	-	-	2	1	**6**	**4**	-	-	-	-	-	-	1	1	1	1	2	1	**4**	**1**
Zeugophorinae	-	-	-	-	-	-	1	1	-	-	-	-	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Cucujiformia/Curculionoidea																												
Anthribidae	4	4	5	3	6	4	29	7	2	1	-	-	**46**	**10**	4	1	8	4	24	4	3	2	3	3	6	2	**48**	**4**
Apionidae	152	9	24	8	60	10	130	10	37	9	53	8	**456**	**11**	51	8	174	12	191	10	184	11	361	10	136	10	**1097**	**13**
Attelabidae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	2	2	-	-	-	-	-	-	**2**	**2**
Brenthidae	-	-	1	1	-	-	-	-	-	-	1	1	**2**	**2**	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**
Curculionidae	114	25	90	11	63	17	433	33	85	13	172	11	**957**	**60**	37	16	58	13	65	16	64	13	79	13	69	11	**372**	**45**
Platypodinae	-	-	-	-	-	-	-	-	-	-	-	-	**-**	**-**	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**
Scolytinae	3	2	1	1	7	3	13	5	2	2	4	3	**30**	**12**	6	2	7	6	11	5	3	3	5	4	2	2	**34**	**17**
Rhynchitidae	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	1	1	-	-	2	2	-	-	-	-	**3**	**3**
Total	**1510**	**223**	**745**	**174**	**1479**	**233**	**1532**	**287**	**521**	**149**	**548**	**122**	**6335**	**556**	**899**	**164**	**915**	**178**	**1320**	**213**	**610**	**145**	**750**	**117**	**598**	**119**	**5092**	**451**

Rain season X. 2002 columns and Dry season I. 2003 columns each comprise sites bus, isi, yal, col, hein, kis and their Sum; the final two columns are the overall Total. Each site reports *n* (individuals) and sp. (species).

Taxa	bus n	bus sp	isi n	isi sp	yal n	yal sp	col n	col sp	hein n	hein sp	kis n	kis sp	Sum n	Sum sp	bus n	bus sp	isi n	isi sp	yal n	yal sp	col n	col sp	hein n	hein sp	kis n	kis sp	Sum n	Sum sp	Total n	Total sp
Larvae	39	-	55	-	76	-	48	-	48	-	28	-	**294**	-	22	-	59	-	31	-	74	-	16	-	17	-	**219**	-	**1113**	-
Adephaga																														
Carabidae	16	7	21	10	15	7	6	3	7	4	3	2	**68**	**15**	27	6	12	5	16	4	-	-	2	2	3	2	**60**	**9**	353	25
Staphyliniformia																														
Histeridae	2	2	-	-	1	1	2	2	1	1	-	-	**6**	**4**	3	2	2	2	-	-	-	-	-	-	-	-	**5**	**3**	25	13
Leiodidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Pselaphidae	1	1	19	6	24	8	3	3	3	2	3	2	**53**	**11**	6	2	14	1	3	2	1	1	7	3	2	2	**33**	**5**	206	15
Ptiliidae	8	2	3	2	3	3	8	2	3	1	-	-	**25**	**4**	5	3	2	1	1	1	-	-	6	3	-	-	**14**	**4**	69	5
Scaphidiidae	104	5	67	5	484	5	34	3	13	4	9	3	**711**	**8**	120	4	17	3	163	4	12	4	11	3	7	3	**330**	**6**	1952	8
Scydmaenidae	63	2	26	3	53	2	3	1	11	2	13	3	**169**	**4**	10	2	10	2	14	2	1	1	9	3	1	1	**45**	**3**	408	5
Staphylinidae	230	34	139	34	215	34	80	27	94	30	93	21	**851**	**69**	384	28	90	25	213	21	51	23	120	25	114	18	**972**	**64**	3598	139
Elateriformia																														
Buprestidae	3	3	-	-	2	1	-	-	1	1	1	1	**7**	**3**	5	2	5	4	7	4	1	1	1	1	1	1	**20**	**6**	53	8
Cantharidae	15	3	13	4	18	5	6	3	2	2	3	2	**57**	**5**	7	4	6	2	2	1	2	2	1	1	1	1	**19**	**5**	134	7
Clambidae	2	1	1	1	2	2	1	1	-	-	1	1	**7**	**4**	4	2	1	1	-	-	-	-	1	1	2	2	**8**	**2**	28	4
Drilidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	**1**	**1**	1	1
Elateridae	14	4	5	2	6	1	1	1	1	1	3	1	**30**	**7**	10	5	8	3	5	2	6	3	1	1	6	2	**36**	**7**	131	13
Eucinetidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Lampyridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	1	1	-	-	**3**	**1**	4	1
Lycidae	2	1	-	-	1	1	-	-	1	1	-	-	**4**	**3**	3	1	1	1	-	-	-	-	-	-	-	-	**4**	**1**	30	12
Ptilodactylidae	5	2	4	3	-	-	2	1	-	-	-	-	**11**	**3**	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**	16	4
Scirtidae	-	-	-	-	-	-	1	1	-	-	-	-	**1**	**1**	-	-	-	-	1	1	-	-	-	-	1	1	**2**	**2**	8	7
Throscidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	**1**	**1**	2	1
Scarabaeiformia																														
Scarabaeidae	4	4	-	-	5	1	-	-	-	-	-	-	**9**	**5**	4	4	6	4	2	2	1	1	1	1	2	2	**16**	**8**	30	9
Bostrichiformia																														
Anobiidae	27	3	1	1	42	3	9	3	1	1	1	1	**81**	**6**	28	4	2	2	30	4	27	4	1	1	1	1	**89**	**9**	245	13
Dermestidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**	1	1
Cucujiformia/Cleroidea																														
Cleridae	-	-	-	-	1	1	3	3	1	1	-	-	**5**	**4**	7	4	2	1	-	-	-	-	-	-	-	-	**9**	**4**	36	11
Melyridae	4	3	-	-	3	1	1	1	2	2	1	1	**11**	**5**	14	4	2	1	1	1	1	1	-	-	1	1	**19**	**4**	52	13
Trogossitidae	4	2	2	1	5	2	-	-	1	1	3	2	**15**	**3**	6	4	8	3	2	2	7	4	3	3	1	1	**27**	**7**	61	9
Cucujiformia/Tenebrionoidea																														
Aderidae	13	7	8	6	18	8	6	3	9	6	2	2	**56**	**17**	17	7	11	7	10	7	5	2	4	3	1	1	**48**	**13**	210	23
Alleculidae	18	3	9	2	2	1	-	-	2	1	2	2	**33**	**3**	2	1	1	1	1	1	1	1	-	-	-	-	**4**	**3**	75	4
Anthicidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Ciidae	-	-	-	-	3	2	2	2	2	-	-	-	**5**	**3**	3	3	1	1	-	-	1	1	1	1	1	-	**6**	**5**	29	19
Colydiidae	2	2	1	1	-	-	-	-	2	1	2	2	**7**	**5**	2	1	1	1	-	-	-	-	-	-	2	1	**5**	**2**	35	10
Lagriidae	7	3	1	1	13	6	2	1	2	2	2	2	**27**	**11**	24	6	7	4	11	3	-	-	1	1	3	3	**46**	**10**	106	24
Meloidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Mordellidae	2	2	7	1	4	3	1	1	-	-	-	-	**14**	**4**	6	5	3	2	1	1	-	-	1	1	-	-	**11**	**5**	42	9
Mycetophagidae	4	2	2	2	3	1	2	2	-	-	4	1	**15**	**2**	9	1	7	3	3	2	-	-	1	1	1	1	**21**	**5**	83	7
Rhipiphoridae	1	1	-	-	1	1	-	-	-	-	-	-	**2**	**1**	-	-	1	1	-	-	-	-	1	1	2	1	**4**	**2**	10	2
Salpingidae	26	2	3	2	26	2	42	2	15	2	6	1	**118**	**2**	10	1	8	1	5	1	6	1	2	1	1	1	**32**	**1**	290	2
Scraptiidae	11	7	18	4	8	5	3	2	13	5	4	2	**57**	**9**	1	1	2	2	1	1	1	1	3	2	1	1	**9**	**3**	122	10
Tenebrionidae	31	6	4	3	12	5	4	2	1	1	3	2	**55**	**11**	20	4	6	6	6	4	1	1	6	3	1	1	**40**	**14**	166	29
Cucujiformia/Cucujoidea																														
Biphyllidae	10	5	16	3	10	3	5	3	13	1	6	2	**60**	**5**	21	5	9	3	5	2	2	2	2	2	6	2	**45**	**5**	249	8
Cerylonidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	2
Coccinellidae	20	11	14	7	24	12	7	5	13	7	18	3	**96**	**25**	28	14	17	8	19	12	14	8	8	7	24	9	**110**	**29**	462	57
Corylophidae	410	15	98	15	281	13	105	11	69	10	105	11	**1068**	**20**	338	13	161	15	241	11	45	8	24	9	67	10	**876**	**19**	4081	27
Cryptophagidae	2	1	2	1	4	3	3	1	8	2	3	1	**22**	**3**	3	1	1	1	2	1	-	-	-	-	-	-	**6**	**1**	63	3
Cucujidae	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**	2	2
Endomychidae	-	-	-	-	2	1	-	-	-	-	-	-	**2**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
Erotylidae	3	2	1	1	9	4	1	1	1	1	1	1	**16**	**6**	-	-	-	-	3	1	-	-	2	1	1	1	**6**	**1**	33	7
Kateretidae	4	1	6	2	3	1	1	1	1	1	-	-	**15**	**2**	4	2	2	1	1	1	4	1	1	1	3	1	**15**	**3**	58	5
Laemophloeidae	10	2	10	3	11	3	4	3	4	3	8	2	**47**	**10**	13	1	9	2	6	3	1	1	-	-	4	2	**33**	**6**	124	16
Languriidae	1	1	2	2	1	1	-	-	1	1	1	1	**6**	**5**	1	1	1	1	5	2	1	1	1	1	1	1	**10**	**5**	34	9
Latridiidae	7	2	2	2	14	1	2	2	3	2	1	1	**29**	**4**	8	3	5	4	3	3	1	1	1	1	2	2	**20**	**6**	102	9
Nitidulidae	2	2	1	1	-	-	1	1	-	-	-	-	**4**	**2**	-	-	-	-	1	1	1	1	-	-	-	-	**2**	**2**	30	15
Phalacridae	8	4	10	6	21	6	19	4	9	3	9	5	**76**	**11**	22	9	10	7	9	5	9	4	11	6	14	5	**75**	**15**	309	18
Propalticidae	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**	-	-	2	1	4	2	1	1	-	-	-	-	**8**	**2**	21	2
Rhizophagidae	-	-	-	-	-	-	-	-	1	1	1	1	**1**	**1**	-	-	-	-	-	-	-	-	1	1	1	1	**2**	**2**	5	4
Silvanidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Sphindidae	9	4	9	1	4	2	4	1	-	-	2	2	**28**	**4**	1	1	-	-	-	-	4	1	-	-	1	1	**6**	**2**	52	4
Cucujiformia/Chrysomeloidea																														
Cerambycidae	41	7	8	4	18	5	4	2	5	2	4	3	**80**	**13**	10	6	4	4	3	3	6	2	-	-	-	-	**23**	**14**	139	26
Alticinae	85	19	79	15	90	18	53	10	42	11	17	8	**366**	**35**	170	13	109	15	128	11	107	15	55	10	60	10	**629**	**31**	1886	47
Bruchinae	-	-	2	1	8	1	2	1	-	-	-	-	**12**	**2**	-	-	-	-	6	3	2	1	2	2	1	1	**11**	**4**	38	6
Cassidinae	2	1	1	1	-	-	-	-	-	-	-	-	**3**	**1**	-	-	-	-	1	1	-	-	-	-	-	-	**1**	**1**	16	4
Chrysomelinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Criocerinae	-	-	-	-	-	-	-	-	-	-	1	1	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3
Cryptocephalinae	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Eumolpinae	9	7	15	10	5	5	4	4	2	2	11	5	**46**	**20**	18	9	12	6	4	4	1	1	1	1	7	6	**43**	**18**	270	33
Galerucinae	20	9	12	9	22	7	5	4	5	4	6	5	**70**	**21**	39	16	29	10	95	11	6	6	5	3	5	3	**179**	**26**	365	37
Hispinae	-	-	-	-	-	-	1	1	-	-	2	1	**3**	**1**	-	-	-	-	-	-	2	2	-	-	-	-	**2**	**2**	15	5
Zeugophorinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	1	-	-	-	**3**	**1**	4	1
Cucujiformia/Curculionoidea																														
Anthribidae	5	5	5	2	9	7	13	5	7	4	4	3	**43**	**13**	7	2	12	6	12	5	11	2	12	4	6	6	**60**	**12**	197	22
Apionidae	177	11	99	11	188	11	64	11	100	10	53	7	**681**	**12**	214	11	108	10	130	10	149	9	147	9	177	11	**925**	**13**	3159	13
Attelabidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
Brenthidae	-	-	-	-	2	1	-	-	-	-	1	1	**3**	**2**	-	-	1	1	1	1	-	-	-	-	1	1	**2**	**2**	7	4
Curculionidae	98	25	140	13	144	19	100	11	107	11	198	16	**787**	**51**	98	15	75	13	159	12	56	11	66	13	106	14	**560**	**46**	2676	115
Platypodinae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Scolytinae	11	5	9	6	20	5	7	4	2	2	1	1	**50**	**15**	3	3	3	3	11	5	10	3	4	4	6	4	**37**	**16**	151	39
Rhynchitidae	1	1	-	-	-	-	-	-	-	-	-	-	**1**	**1**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	3
Total	**1556**	**256**	**895**	**210**	**1861**	**242**	**627**	**156**	**579**	**150**	**611**	**134**	**6129**	**524**	**1736**	**237**	**809**	**204**	**1351**	**182**	**554**	**133**	**533**	**142**	**648**	**140**	**5631**	**502**	**23187**	**1023**

Appendix 7: Rarefaction plot of total numbers of predacious beetles (top) and mycetophagous beetles (bottom)
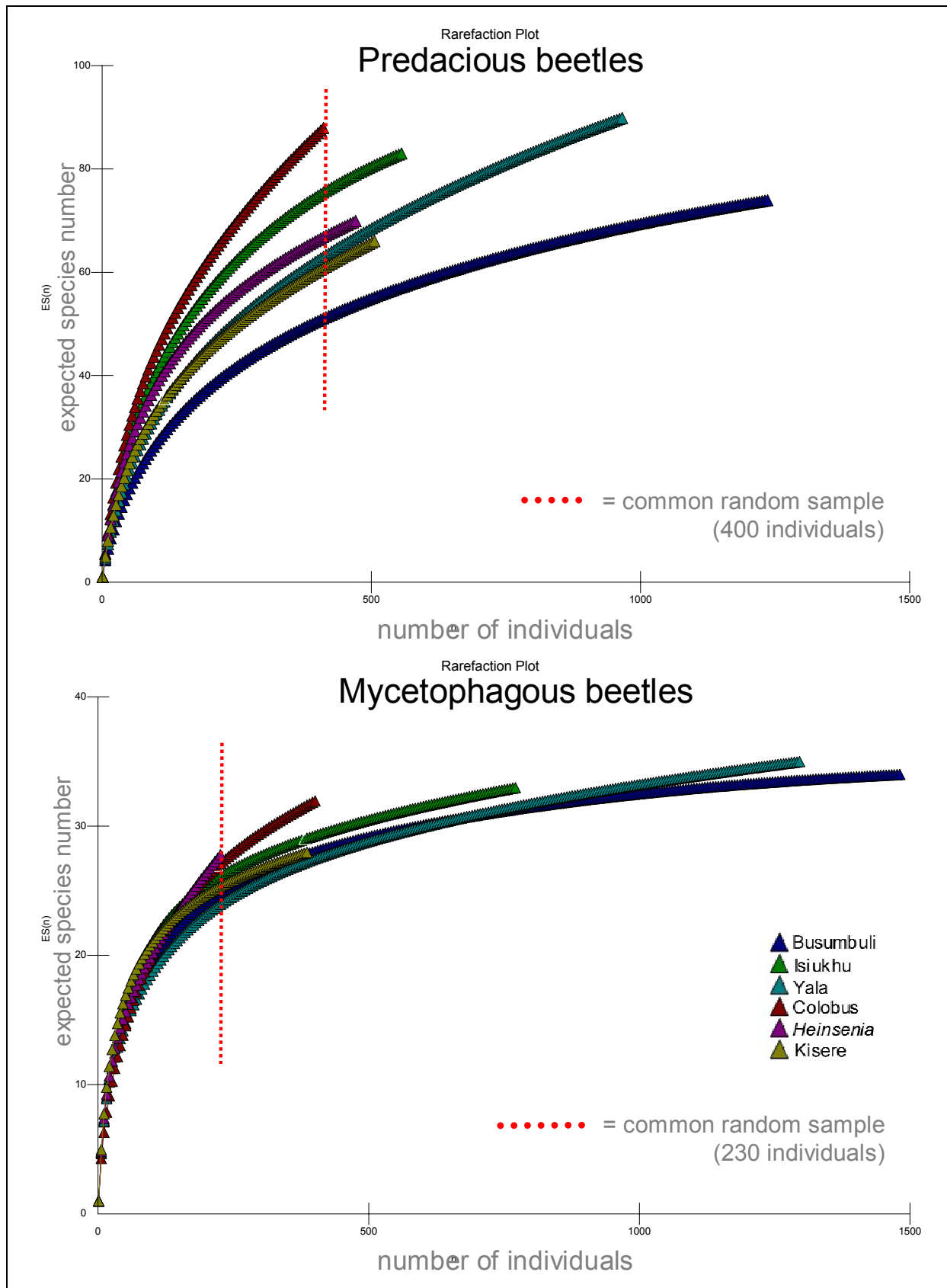
Appendix 8: Rarefaction plot of total numbers of leaf beetles (top) and weevils (bottom)
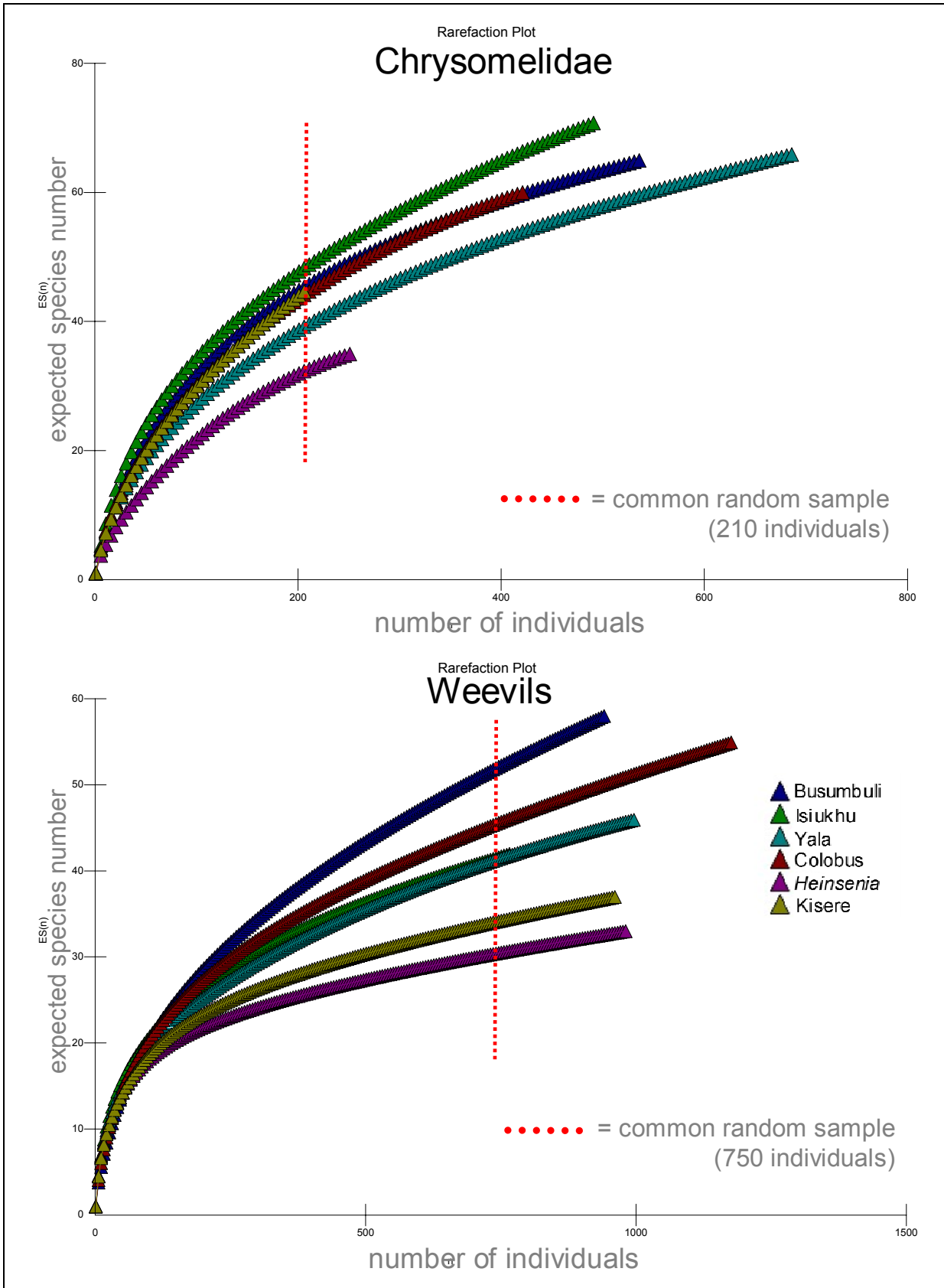
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