Tropical Ecology 37(2): 203-213, 1996
© International Society for Tropical Ecology
ISSN 0564-3295

The community structure of arthropods in virgin and managed sites in the Kibale Forest, Western Uganda

MATTI NUMMELIN

Department of Ecology and Systematics, Division of Environmental Biology, P.O. Box 7 (Unionink. 44), FIN-00014, University of Helsinki, Finland

Abstract: The structure of arthropod communities in the forest floor vegetation in five different forest sites in Kibale Forest, Western Uganda, was studied by monthly sweep net sampling during a 23 month period (June 1983 - May 1985). Additional samples were taken one year (Sept. 1986) and six years (Sept. 1991) later. The studied habitats included two virgin forest sites, two selectively logged sites and one exotic pine plantation. The community structure of arthropods changed relatively little through the study period. Nine groups (Araneae, Hymenoptera, Heteroptera, Homoptera, Coleoptera, Orthoptera, Lepidoptera, caterpillars (Lepidoptera and Hymenoptera: Symphyta larvae) form over 95% of all the arthropod individuals caught. Arthropod groups have different responses to seasonal rainfall. In canonical correspondence analysis over the seasons and habitats, Heteroptera and Araneae, Coleoptera and caterpillars, as well as Diptera and Lepidoptera are fairly close to each other in the principal component axes. When number of individuals in each group is used as a variable in the canonical correspondence analysis the intensity of forest management affects significantly the variation in the arthropod community structure; rainfall does not significantly affect the percentile makeup of arthropod populations, but affects significantly the total numbers of arthropods.

Resumen: Se estudió la estructura de las comunidades de artrópodos del suelo en cinco diferentes sitios en un bosque en Kibale, Oeste de Uganda, a través de un muestreo mensual por arrastre neto durante el período de Junio de 1983 a Mayo de 1985. Se tomaron muestras adicionales un año después (Septiembre de 1986) y seis años después (Septiembre 1991). Los habitats estudiados incluyeron dos sitios en un bosque maduro, dos sitios registrados selectivamente y una plantación de pinos exóticos. La estructura de la comunidad de artrópodos cambió relativamente poco a través del período de estudio. Nueve grupos forman el 95% de todos los individuos capturados: Araneae, Hymenoptera, Heteroptera, Homoptera, Coleoptera, Orthoptera, Lepidoptera, orugas (Lepidoptera e Hymenoptera: Larvas de *Symphyta*). Los grupos de artrópodos tienen diferentes respuestas a la precipitación estacional. Un análisis de correspondencia canónica entre las estaciones y habitats, mostró más estrechamente relacionados en el eje de componentes principales a Heteroptera y Araneae, Coleoptera y las orugas así como entre Diptera y Lepidoptera. Cuando se usó el número de individuos en cada grupo como variable en el análisis canónico de correspondencia, la intensidad del manejo del bosque afectó significativamente la variación en la estructura de la comunidad de artrópodos; la precipitación no afectó significativamente la composición porcentual de la comunidad de artrópodos, pero sí afectó significativamente el número total de artrópodos.

Résumé: La structure des communautés d'arthropodes dans les sols forestiers de 5 stations différentes de la forêt de Kibale (Ouest de l'Ouganda) a été étudiée pendant 23 mois (Juin 1983-Mai 1985) au moyen d'un échantillonnage mensuel au filet. D'autres échantillons ont été collectés un an (Sept. 1986) et six ans (Sept. 1991) plus tard. Les sites étudiés sont: deux forêts naturelles non perturbées, deux forêts exploitées sélectivement, et une plantation de pins exotiques. La structure de la communauté d'arthropodes a peu

changé au cours de la période d'étude. Neuf groupes (Ananeae, Hyménoptères, Hétéroptères, Homoptères, Coléoptères, Orthoptères, Lépidoptères, chenilles (Lépidoptères et Hyménoptères: larves de *Symphyta*) constituent 95% de tous les individus capturés. Ces groupes ont des réponses différentes aux variations saisonnières de la pluviométrie. Dans l'analyse canonique des correspondances sur les saisons et les habitats, les Ananeae et les Hétéroptères, les Coléoptères et les chenilles, les Diptères et les Lépidoptères sont proches les uns des autres sur les axes principaux. Quand le nombre des individus dans chaque groupe est utilisé comme variable dans l'analyse canonique des correspondances, l'intensité de la gestion forestière affecte significativement la structure de la communauté des arthropodes; la pluviométrie n'influence pas les proportions des différentes populations, mais modifie fortement les effectifs totaux.

Resumo: A estrutura das comunidades de artropodes na vegetação do solo florestal em cinco estações florestais diferentes da floresta de Kibale no Uganda ocidental foi estudada mensalmente mediante uma amostragem de passagem com rede durante um período de 23 meses (Jũnho 1983 - Maio 1985). Os habitats estudados incluíram duas estações florestais virgens, duas onde se praticaram abates selectivo e umo com uma plantação exótica de pinheiro. A estrutura da comunidade dos artropodes mudou relativamente pouco ao longo do período de estudo. Nove grupos (Araneae, Hymenoptera, Heteroptera, Homeptera, Coleoptera, Orthoptera, Lepidoptera e largartas (Lepidoptera e Hymenoptera: larva de *Symphyta*)) formam cerca de 95% de todos os artropodes apanhados. Os grupos de artropodes apresentam diferentes respostas à queda pluviométrica sazonal. Uma análise canónica de correspondências sobre as estações e habitats evidenciou que os Heteroptera e Araneae, Coleoptera e lagartas, bem como os Diptera e os Lepidoptera estão muito próximos uns dos outros no eixo das componentes principais. Quando o número de indivíduos em cada grupo é utilizado como variável na análise de correspondências canónicas, a intensidade do ordenamento florestal afecta significativamente a variação da estrutura da comunidade dos artropodes; a queda pluviométrica não afceta significativamente o percentil da composição da população dos artropodes se bem que afecte significativamente o seu número total.

Key Words: Africa, arthropods, forest management, insects, Kibale, logging, seasonality, Uganda.

Introduction

Data documenting arthropod diversity in the tropics are scarce (Hammond 1990; Stork & Brendell 1993) papers on insect diversity in African rain forests are virtually nonexistent. The main focus of insect studies in tropical forests has been on forest plantations and pest species (e.g., Loyttyniemi 1988 and references therein). The arthropods in clear-cuts (Cambefort 1984; Howden & Nealis 1975) as well as selectively logged sites have been studied to some degree (Holloway 1987; Nummelin 1989, 1992; Nummelin & Borowiec 1991; Nummelin & Fürsch 1992; Nummelin & Hanski 1989; Wolda 1987; Wolda et al. 1983). However, little information is available on the effects of different types of forest management on arthropod communities.

This study reports the results of a two-year intensive study plus two additional samples one and six years later, comparing the arthropod communities of two natural forest sites (K30 and Ngogo, Fig. 1), two selectively logged sites (K14 and K15) and an exotic pine plantation in the Kibale Forest, Western Uganda. A description of the effects of tropical forest management on arthropod communities and an explanation of the observed differences between virgin and managed sites is a main focus of this study. This report is part of a long-term project studying the ecological effects of forestry practices in Kibale Forest. The project has yielded published results on tree falls (Skorupa & Kasenene 1984; Kasenene & Murphy 1991), primates (Skorupa 1986; Struhsaker 1975), small rodents (Basuta & Kasenene 1987; Kasenene 1984), arthropods (Nummelin 1986), dung beetles,

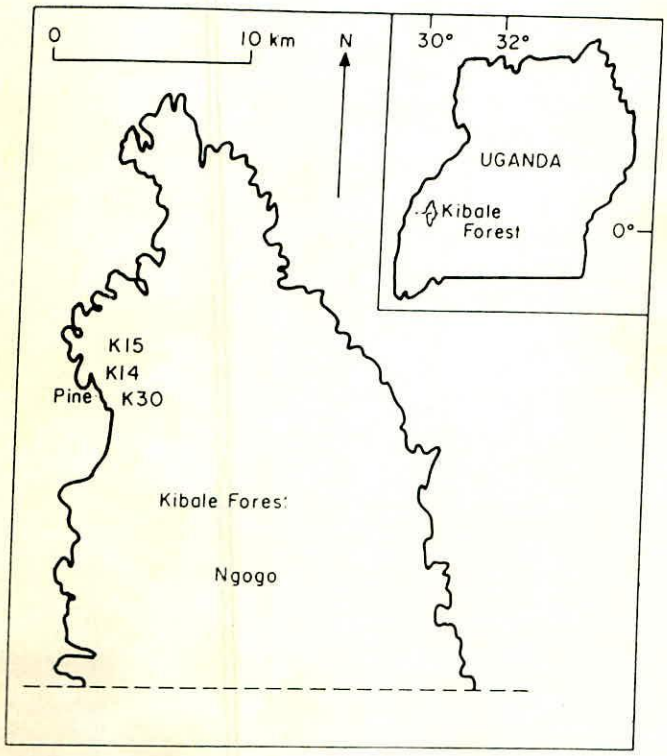

Fig.1. The geographical location of the Kibale Forest and the study sites.

(Nummelin & Hanski 1989), coccinellids (Nummelin & Fürsch 1992), Cassidinae (Nummelin & Borowiec 1991), arthropod herbivory (Nummelin 1992; Nummelin & Roininen 1996), and elephants, duikers and bushpigs (Nummelin 1990).

Struhsaker (1987) presented a flow chart model of the ecological effects of logging in the Kibale Forest. One aim of the present study was to test whether there are differences in the arthropod communities of logged and virgin areas, as the model predicts.

Wolda (1983 a, b) has concluded that insect populations are at least as unstable in the tropics as in temperate regions. His conclusion was mainly based on the observations of neotropical insect populations. This study allows an assessment of the stability of arthropod abundances between years in an African forest. Nummelin & Fürsch (1992) have shown great year to year fluctuations in coccinellid populations in Kibale.

Specifically, this study attempted to answer the following questions: (1) how stable are the abundances of forest-floor arthropods over the seasons and years; (2) are there differences in arthropod communities in differently managed forest sites; and (3) how do different arthropod groups respond to seasonally varying rainfall?

Study sites

Kibale Forest is a medium-elevation (ca. 1500 m) moist evergreen forest, 560 km^2 in area, located in western Uganda (0°13' to 0°41' N and 30° 19' to 30° 32'E) (Fig. 1). Yearly rainfall is roughly 1500 mm. It has two dry and two rainy seasons per year (Fig. 2). Kibale differs from lowland tropical rain forest in having lower minimum temperature (ca. +11°C), and lower rainfall, but otherwise it possesses most of the typical structural features of lowland forests (Langdale-Brown et al. 1964). The forest topography is gently undulating, replaced by swamps and rivulets in low-lying areas and by grasslands on hilltops in some disturbed places.

In 1969, mechanized selective felling was applied to ca. 35% of the northern and central forest area. During my study, 15-20 years after logging, logged areas were still easily recognizable due to the large gaps. Forest compartment K15 (Fig. 1) was more heavily logged (ca. 21 m^3ha^{-1}) than compartment K14 (14 m^3ha^{-1}) (Skorupa & Kasenene 1984). Both logged sites had denser forest floor vegetation than virgin sites, especially during the late rainy season (Nummelin 1992).

Some areas adjacent to the forest were planted with exotic conifers in 1969. Since then there has not been any other forest management in the area. The plantation study site was composed of 20-year-old non-native *Pinus caribaea* Morolet. The exotic pine plantation had quite lush forest floor vegetation which is unusual by comparison with more typical, bare ground pine plantations in Uganda (Struhsaker 1987).

Virgin and managed study sites are described in more detail by Nummelin (1992).

Methods

Arthropod samples were collected by sweep netting in all five sites on a monthly basis. Each sample consisted of 800 sweeps. the sweep net was a standard

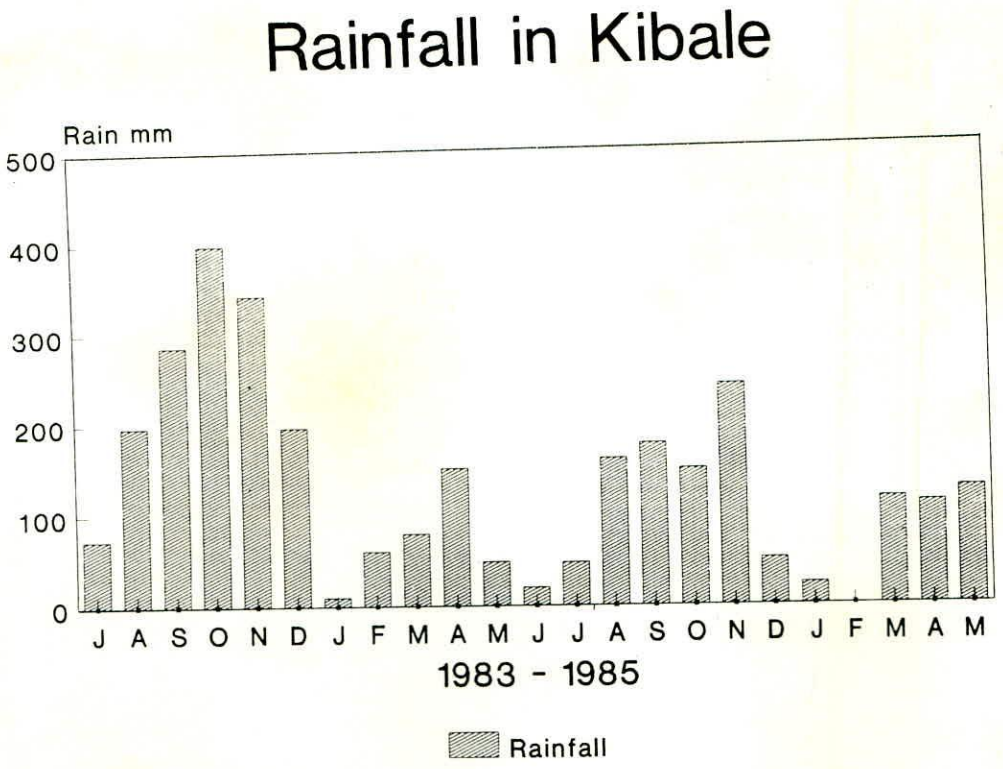

Fig.2. Rainfall in Kibale Forest 1983-1985.

38-cm diameter muslin insect net with 61-cm handle (see Janzen 1973a). All study sites had a 50 x 50 m trail grid system which was cut some years prior to the study period. One half of the sweeps were taken from the trail sides and the other half were taken from intact sites within the trail grid. However, all samples from Ngogo were taken from intact sites. Sweeps were made only in places where the net could hit forest floor vegetation. Thus, open gaps in forest floor vegetation were avoided. Depending on the height of the vegetation, the minimum sweeping height varied from 20 to 80 cm. Sweeping took place on dry early afternoons having no morning showers. For more details on the sweeping method and equipment used see Janzen (1973a).

Results

The number of arthropod individuals in the sweep net samples varied greatly within habitats depending on season (Fig. 3 a-e). There are significant correlations between total numbers of arthropods caught and rainfall (see Nummelin 1989). The logged sites had greater extremes in abundance than the virgin sites. The peaks of arthropod abundance during the rainy season occurred earlier in the logged sites than in the virgin forest (Nummelin 1989). In pairwise comparison of catches during the same month (Wilcoxon matched-pairs, Siegel 1956), natural sites K30 and Ngogo had fewer arthropods than logged sites K14 and K15 and the exotic pine plantation. This comparison is most applicable to virgin K30 and logged K14 and K15 which are close to each other and at similar elevations (Table 1).

One can not detect clear seasonal changes in the relative abundances of different arthropod groups (Fig. 3 a-e). (However, see later correlations of each arthropod group with rainfall). The nine most common groups: Araneae (Opiliones not included since they occurred only occasionally), Hymenoptera (mainly *Formicidae: Crematogaster* spp.), Heteroptera, Homoptera, Coleoptera, Orthoptera, Lepidoptera, caterpillars (Lepidoptera and Hymenoptera: *Symphyta* larvae) formed over 95% of all the arthropod fauna caught by sweep net from the forest floor vegetation in the Kibale Forest. The group "others" mainly consisted of Phasmidae, Mantidae and Blattidae.

When arranging the nine most common arthropod groups (+group "others") by canonical correspondence analysis over the seasons and habitats the relative distances of Heteroptera and Araneae, Coleoptera and caterpillars as well as Diptera and Lepidoptera are closer to each other than the mean nearest neighbour distances of groups along the principal component axes. None of the other groups aggregated in the analysis (Fig. 4). This indicates that there is closer correspondence in the variation of individual numbers between sites and over seasons of Heteroptera and Araneae, Coleoptera and caterpillars as well as Diptera and Lepidoptera than of the other arthropod groups.

The intensity of forestry practices accounts for the significance of the variation of arthropod community structure in the canonical correspondence analysis.

The percentage similarity index (Renkonen index, Wolda 1981) varied between 61% and 95% for samples from different habitats taken during the same month. No seasonal or between-habitat trends were detectable by the similarity indices, and the indices seemed to vary in random manner.

When the responses of different arthropod groups to the 30-day cumulative rainfall (roughly the larval development time of an arthropod) was studied in four sites, those studied for 23 months, by correlation analysis, with the time lags of 0, 15, 30, 60, 90, days (i.e. cumulative rainfall 29-0, 44-15, 59-30, 89-60 and 119-90 days previous to the sampling day), more singificant correlations were obtained than expected by chance (Table 2). The regression models in Table 1 can be used to predict the numbers of arthropods in different habitats in Kibale Forest when the rainfall is known. For example, the expected number of individuals (y) of Araneae in 800 sweep samples in logged forest is 0.12 x (cumulative rainfall 89-60 days previous the sampling day) + 49.

Different responses were detected between arthropod groups as well as within an arthropod group, between the different sites. In general, the best correlations were in logged forest with 30-day time lag and in virgin forest and pine forest with 90-day time lag. In Acridiade and Formicidae, no correlation with the rainfall was found; indicating that the numbers of grasshoppers and ants in the forest floor vegetation can not be predicted on the basis of comulative local rainfall in Kibale Forest. The peak of arthropod abundance during late 1983 seemed to be somewhat higher than in other times.

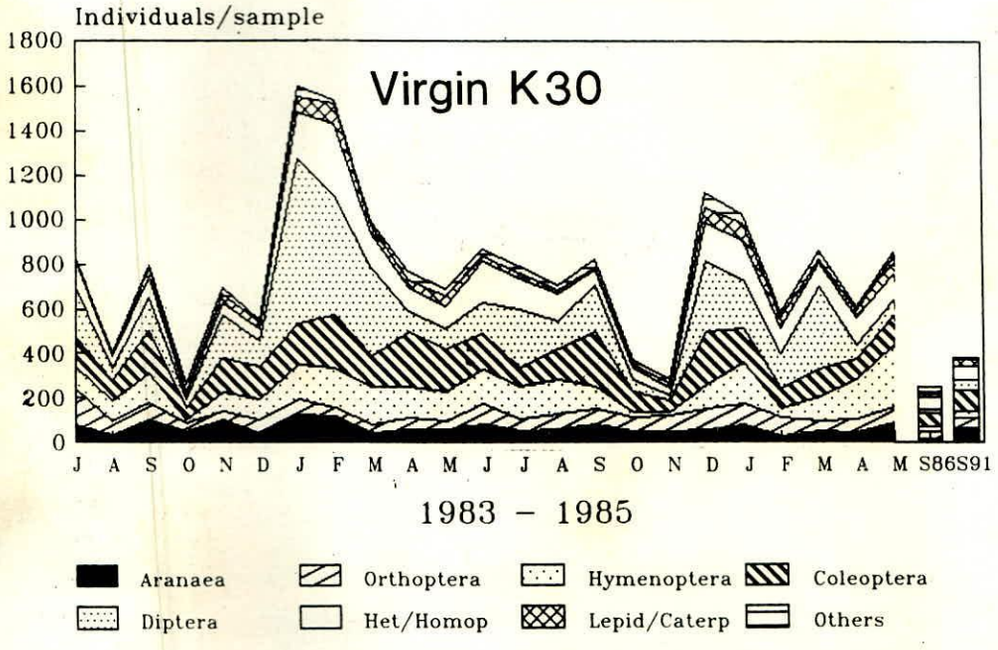

Fig.3a. The numbers of individuals in nine most common arthropod groups (+group "others") in the sweep net samples in virgin K30 habitat in the Kibale Forest.

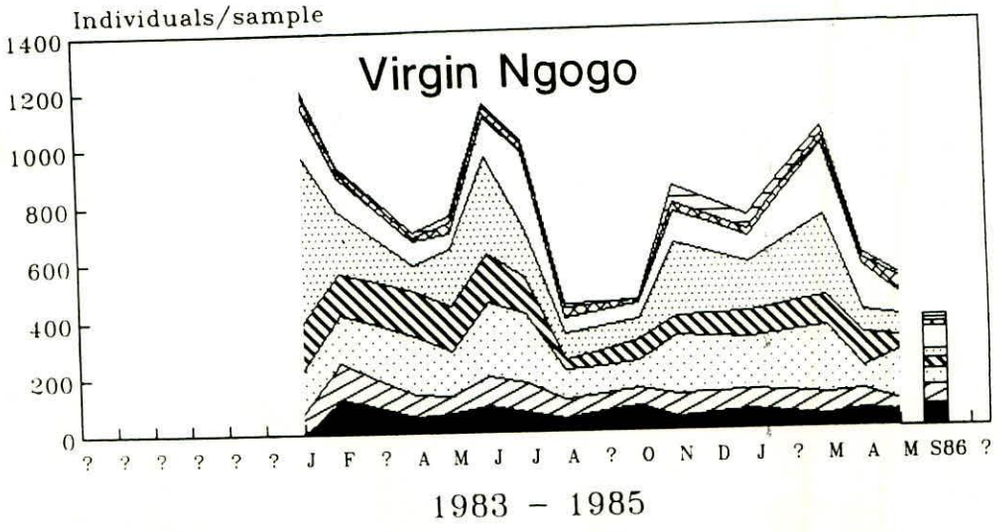

Fig.3b. The numbers of individuals in nine most common arthropod groups (+group "others") in the sweep net samples in virgin Ngogo habitat in the Kibale Forest (For code see Fig. 3a).

Discussion

This study supported Struhsaker's (1987) flow-chart model predicting higher numbers of arthropods in logged sites. Struhsaker (1987) suggests this to be due to the denser forest floor vegetation in logged sites. According to this study Struhsaker's model holds best during the rainy seasons when the forest floor vegetation is most dense in the logged sites (Nummelin 1989). Struhsaker's (1987) model helps to explain the poor tree regeneration in the logged sites in the Kibale Forest where arthropod numbers are highest. In logged sites, the possible effects of arthropods on tree regeneration should be studied in more detail, taking into consideration different tree species and their herbivores (see Nummelin 1992; Nummelin & Fürsch 1992; Nummelin & Roininen 1997).

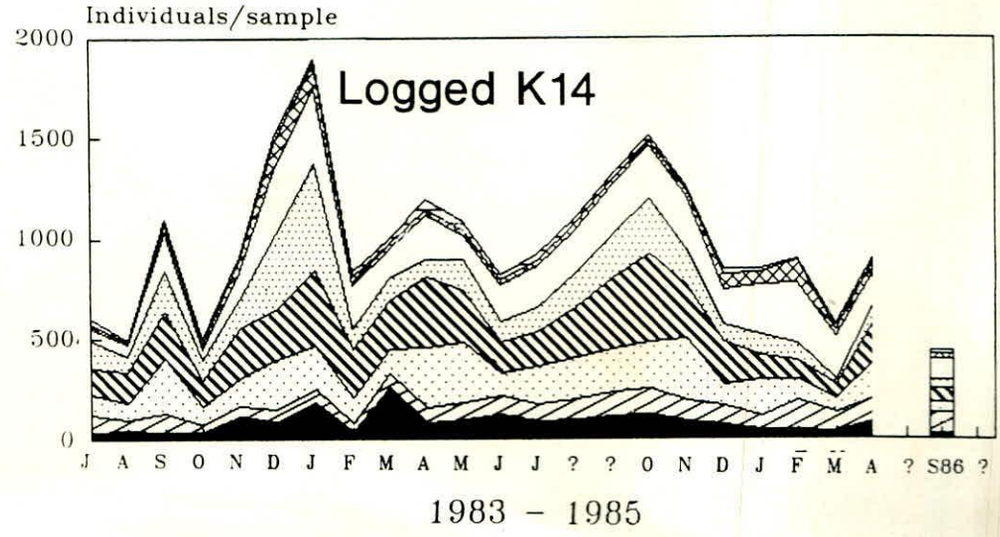

Fig.3c. The numbers of individuals in nine most common arthropod groups (+group "others") in the sweep net samples in Logged K14 habitat in Kibale Forest (For code see Fig. 3a).

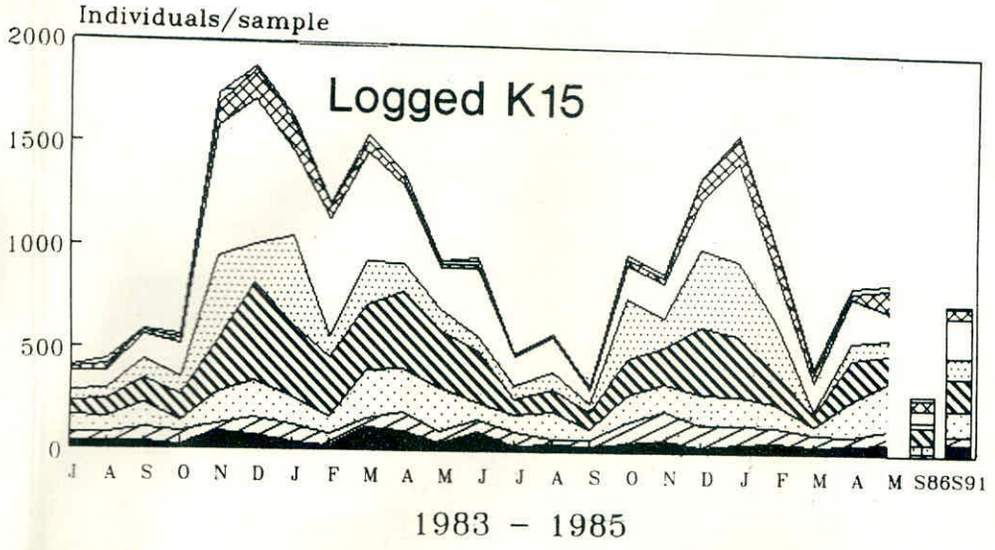

Fig.3d. The numbers of individuals in nine most common arthropod groups (+group "others") in the sweep net samples in logged K15 habitat in Kibale Forest (For code see Fig. 3a).

The total number of all arthropods caught in 800 sweep samples is of the same magnitude as obtained in similar sweep net samples in secondary vegetation taken in Osa, Taboga and San Vito in Costa Rica (Janzen & Pond 1975). However, the numbers are less than those recorded in mid summer in secondary vegetation in Michigan and England in the temperate zone (Janzen & Pond 1975). This suggests that arthropods are rarer in tropical forest floor vegetation than in a temperate meadow in mid-summer. The community structure of arthropods in Kibale resembles the community structure of the samples obtained by sweep netting in the Neotropics (Boinski & Fowler 1989; Elton 1973; Janzen 1973a, b; Janzen & Schoener 1968; Janzen et al. 1976; Nentwig 1989; Tanaka & Tanaka 1982). Published results on sweep net sampling in forest sites in Old World tropics are not available for comparison.

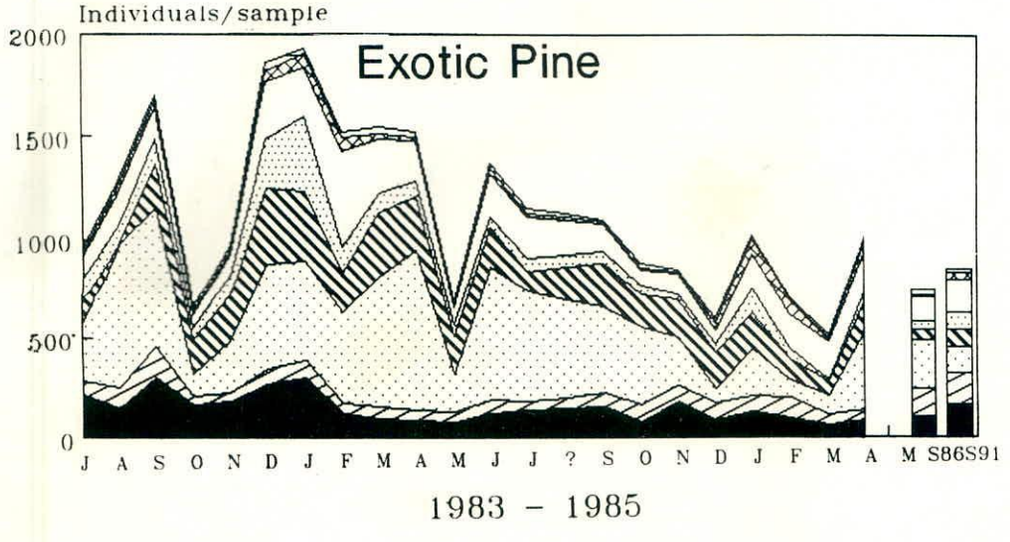

Fig.3e. The numbers of individuals in nine most common arthropod groups (+group "others") in the sweep net samples in pine plantation in Kibale Forest (For code see Fig 3a).

Table 1. Summary of results for Wilcoxon matched-pairs test for arthropod abundances in different habitats in Kibale Forest, Uganda (K30, Ngogo: virgin sites; K14, K15 logged sites; Pine, exotic Pine plantation).

Forest compared	n	z	p (2-tailed)	Comment
K30 vs K14	20	2.07	0.038	K14>K30
K30 vs K15	23	1.78	0.075	K15>K30
K14 vs K15	20	0.22	0.823	K14=K15
K15 vs Ngogo	13	1.40	0.162	K15>Ngogo
K30 vs Ngogo	13	0.97	0.529	K30=Ngogo
K14 vs Ngogo	11	1.47	0.142	K14>Ngogo
Pine vs Ngogo	12	2.08	0.038	Pine>Ngogo
Pine vs K30	22	3.02	0.003	Pine>K30
Pine vs K15	22	0.97	0.330	Pine=K15
Pine vs K14	20	1.51	0.130	Pine>K14

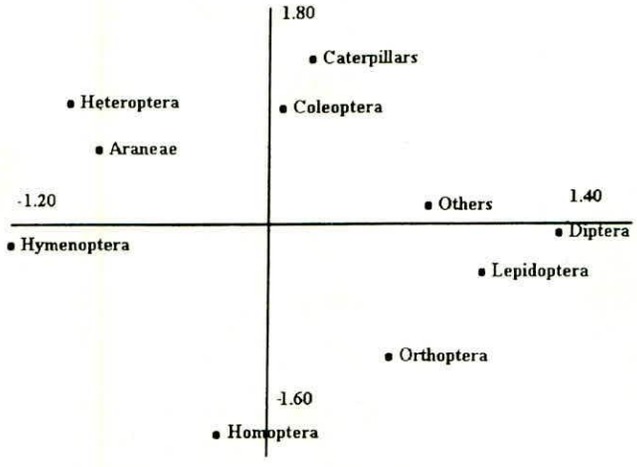

Fig.4. The nine most common arthropod groups (+group "others") in the sweep net samples during 23 months from forest floor vegetation in the Kibale Forest arranged by canonical correspondence analysis (1. and 2. principal components).

When the results of this study are compared to arthropod samples from the herb-layer vegetation from a rain forest in South East Asia collected by vacuum sampler (Stork & Brendell 1993), Kibale seems to harbour less Thysanoptera, Psocoptera, Collembola and Acarina. However, the sweep method used in Kibale is much rougher on specimens than vacuum sampling. No vacuum sampler was available in Uganda at the time of this study. All the above mentioned arthropod groups are small and mostly soft bodied, thus they are often destroyed by the sweep method. Sweep-netting is notoriously selective in favor of larger insects (Hespenheide 1979). For further discussion of restric-

Table 2. The significant correlations(P<0.05, NS=non-significant and linear regression equations for the number of individuals in most common arthropod groups in sweep net samples (y) to the 30 days cumulative rainfall (x) with time lag (the highest correlation to 0, 30, 60 or 90 day-time lag is indicated in the Table) in four different habitats (over a 23 month study period) in Kibale Forest, r indicates the correlation coefficient. See further explanations in the text.

	lag, days	y=ax+b		r
		a	b	
Virgin K30				
Araneae	60	0.12	49	0.45
Orthoptera	NS			
Acrididae	NS			
Homoptera	90	0.44	56	0.68
Heteroptera	NS			
Hemipt. larvae	60	0.04	8	0.38
Hymenoptera	90	0.22	78	0.48
Formicidae	NS			
Wasps	90	0.20	30	0.56
Coleoptera	NS			
Diptera	90	1.20	39	0.74
Lepidoptera	90	0.10	0	0.65
Lepid./Hym. larvae	90	0.07	11	0.64
Logged K15				
Araneae	NS			
Orthoptera	60	0.09	58	0.32
Acrididae	NS			
Homoptera	30	0.86	166	0.59
Heteroptera	30	0.59	31	0.62
Hemipt. larvae	30	0.13	20	0.55
Hymenoptera	NS			
Formicidae	NS			
Wasps	90	0.16	33	0.50
Coleoptera	30	0.40	153	0.41
Diptera	30	0.65	83	0.61
Lepidoptera	30	0.08	8	0.53
Lepid./Hym. larvae	30	0.13	15	0.58

Contd.

Table 2 contd.

	lag, days	y=ax+b a	b	r
Logged K14				
Araneae	30	0.18	53	0.52
Orthoptera	NS			
Acrididae	NS			
Homoptera	NS			
Heteroptera	90	0.25	44	0.58
Hemipt. larvae	NS			
Hymenoptera	NS			
Formicidae	NS			
Wasps	90	0.18	23	0.50
Coleoptera	30	0.39	162	0.45
Diptera	30	0.83	39	0.78
Lepidoptera	NS			
Lepid./Hym. larvae	30	0.15	12	0.59
Exotic Pine				
Araneae	30	0.28	109	0.51
Orthoptera	NS			
Acrididae	NS			
Homoptera	90	0.71	76	0.73
Heteroptera	90	0.29	37	0.69
Hemipt. larvae	NS			
Hymenoptera	NS			
Formicidae	NS			
Wasps	90	0.07	14	0.50
Coleoptera	30	0.36	143	0.57
Diptera	30	0.34	47	0.52
Lepidoptera	90	0.06	3	0.62
Lepid./Hym. larvae	90	0.11	7	0.63

tions in the sweep method, see e.g. DeLong (1932); Beall (1935); Janzen (1973a).

The effect of forestry practices in Kibale Forest could be detected by the pairwise comparison of total numbers of arthropods caught in differently managed sites as well as by canonical correspondence analysis. However, the effect of forestry intensity on the community structure in this multivariate analysis was so complex that it could not be visualized using two or three principal components as axes. The between-habitat differences are obscure in the percentile similarity indices as well. Janzen (1973b) detected a reduction of Hemiptera-Heteroptera bugs in sweep net samples from virgin to secondary sites in Costa Rica. No such reduction is detectable in Kibale.

The responses of different arthropod groups to rainfall have different time lags both within and between the habitats. It is also known that the species composition may vary between sampling habitats (Nummelin & Borowiec 1991; Nummelin & Fürsch 1992). Thus, it is hard to make any generalizations at the community level. The general trend with logged areas having a 30-day time lag and virgin and pine forests having 90-day time lags agrees with previous results when the total number of arthropods in these samples was correlated with rainfall (Nummelin 1989). Tanaka & Tanaka (1982) reported an approximate 3-week time lag relative to rainfall in the correlation of abundance of various insect groups in a West Indian island, Grenada. Thus the response in insect numbers to the rainfall in Grenada appears to be quicker than that in Kibale Forest.

The higher peaks of arthropod numbers in Kibale in late 1983 may be caused by climatic factors associated with El Nino during that year. The year was exceptionally hot and wet (Struhsaker 1997). Nummelin & Fürsch (1992) have documented some mass occurrences of Coccinellid species during late 1983 and early 1984. Those species were rare or nonexistent in earlier or later samples.

In brief, this study gives the following answers to the questions posed in the introduction: There is great seasonal variation in the abundances of arthropod groups in the Kibale Forest. Practically all groups correlate positively with rainfall, however, time lags in response vary between groups and habitats. The between-year variation of arthropod abundances may reflect macroclimatic chages. Forest management does affect the community structure of forest floor arthropods in the Kibale Forest.

Acknowledgements

I wish to thank the National Research Council of Uganda, the Forest Department, and the President's office for permission to conduct research in Uganda. The study was financially supported by the Kibale Forest Project (New York Zoological Society) and the Academy of Finland. Jouko Sarvala did the canonical correspondence analysis. Comments by J.A. Bullock, J. Niemela, P. Murphy, T. Struhsaker and three referees improved the manuscript.

References

Basuta, I. & J.M. Kasenene. 1987. Small rodent populations in selectively felled and mature tracts of Kibale Forest, Uganda. *Biotropica* **19**: 260-266.

Beall, G. 1935. Study of arthropod populations by method of sweeping. *Ecology* **16**: 216-225.

Boinski, S. & N.L. Fowler. 1989. Seasonal patterns in a tropical lowland forest. *Biotropica* **21**: 223-233.

Cambefort, Y. 1984. *Étude écologique des Coléopterés Scarabaeidae de Cote d' Ivoire*. Ph. D. Thesis. University Abidjan, Ivory Coast.

DeLong, D.M. 1932. Some problems encountered in the estimation of insect populations by sweeping method. *Annals Entomological Society of America* **25**: 13-17.

Elton, C.S. 1973. The structure of invertebrate populations inside neotropical rain forest. *Journal of Animal Ecology* **42**: 55-104.

Hammond, P.M. 1990. Insect abundance and diversity in the Dumoga- Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. pp. 197-253. *In*: W.J. Knight & J.D. Holloway (eds.) *Insects and the Rain Forests of South East Asia (Wallacea).* The Royal Entomological Society of London.

Hespenheide, H.A. 1979. Are there fewer parasitoids in the tropics? *American Naturalist* **113**: 766-799.

Holloway, J.D. 1987. Macrolepidoptera diversity in the Indoaustralian tropics: geographic, biotopic and taxonomic variations. *Biological Journal of Linnean Society* **30**: 325-341.

Howden, H.F. & V.G. Nealis. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* **7**: 77-83.

Janzen, D.H. 1973a. Sweep samples of tropical foliage insects: Description of study sites, with data on species abundances and size distribution. *Ecology* **54:** 661-686.

Janzen, D.H. 1973b. Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* **54**: 687-708.

Janzen, D.H. & C.M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. *Transactions of the Royal Entomological Society, London* **127**: 33-50.

Janzen, D.H., M. Ataroff, M. Farinas, S. Reyes, N. Rincon, A. Soler, P. Soriano & M. Vera. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* **8**: 193-203.

Janzen, D.H. & T.W. Schoener. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* **49**: 96-110.

Kasenene, J.M. 1984. The influence of selective logging on rodent populations and the regeneration of selected tree species in the Kibale Forest, Uganda. *Tropical Ecology* **25**: 179-195.

Kasenene, J.M. & P.G. Murphy. 1991. Post-logging tree mortality and major branch losses in Kibale Forest, Uganda. *Forest Ecology and Management* **46**: 295-307.

Langdale-Brown, I., H.A. Osmaston & J.G. Wilson. 1964. *The Vegetation of Uganda.* Government Printing Office Entebbe.

Löyttyniemi, K. 1988. Status of forest insects in tropical forest plantations. (in Finnish, English summary). *Silva Carelica* **12**: 121-132.

Nentwig, W. 1989. Seasonal and taxonomic aspects of the size of arthropods in the tropics and its possible influence on size- selectivity in the prey of a tropical spider community. *Oecologia* **78**: 35-40.

Nummelin, M. 1989. Seasonality and effects of forestry practices on forest floor arthropods in the Kibale Forest, Uganda. *Fauna Norvegica* Ser. B **36**: 17-25.

Nummelin, M. 1990. Relative habitat use of duikers, bush pigs and elephants in virgin and selectively logged areas in Kibale Forest, Uganda. *Tropical Zoology* **3**: 111-120.

Nummelin, M. 1992. Invertebrate herbivory in the forest floor vegetation of virgin and managed forest sites in the Kibale Forest, Western Uganda. *African Journal of Ecology* **30**: 213-222.

Nummelin, M. & L. Borowiec. 1991. Cassidinae beetles in virgin and managed forests in Kibale Forest, Western Uganda. *African Journal of Ecology* **30**: 10-17.

Nummelin, M. & H. Fürsch. 1992. Coccinellids in virgin and managed forests in Kibale Forest, Western Uganda. *Tropical Zoology* **5**: 155-166.

Nummelin, M. & I. Hanski. 1989. Dung beetles in virgin and managed forests in Kibale Forest, Western Uganda. *Journal of Tropical Ecology* **5**: 349-352.

Nummelin, M. & H. Roininen. 1997. *Herbivorous leaf damages in two forest floor plants Achyrantes aspera L. and Pollia condensata C.B.Cl. in virgin and managed sites in the Kibale Forest*, Western Uganda.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences.* McGraw-Hill Kogakusha, Ltd., Tokyo.

Skorupa, J.P. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. pp. 57-70. *In:* K. Benirschke (ed.) *Primates, the Road to Self-Sustaining Populations.* Springer Verlag, New York.

Skorupa, J.P. & J.M. Kasenene. 1984. Tropical forest management: can rates of natural treefalls help guide us? Oryx **18**: 96-101.

Stork, N.E. & M.D.J. Brendell. 1993. Arthropod abundance in lowland rainforest of Seram. pp. 115-130. *In*: J. Proctor & I. Edwards (eds.) *Natural History of Seram.* Intercept, Hampshire, U.K.

Struhsaker, T.T. 1975. *The Red Colobus Monkey.* University Chicago Press, Chicago.

Struhsaker, T.T. 1987. Forestry issues and conservation in Uganda. *Biological Conservation* **39**: 209-234.

Struhsaker, T.T. 1997. *Kibale: A Case Study of Logging in a Tropical Forest*. Florida University Press.

Tanaka, L.K. & S.K. Tanaka. 1982. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic Island. *Biotropica* **14**: 114-123.

Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* **50**: 296-302.

Wolda, H. 1983a. "Long-term" stability of tropical insect populations. *Researches on Population Ecology Suppl.* **3**: 112-126.

Wolda, H. 1983b. Spatial and temporal variation in abundance in tropical animals. pp. 93-105. In: S.L. Sutton, T.C. Whitmore & A.C. Chadwick. (eds.) *Tropical rainforest: Ecology and management*. Blackwell Science Publication, Oxford.

Wolda, H. 1987. Altitude, habitat and tropical insect diversity. *Biological Journal of Linnean Society* **30**: 313-323.

Wolda, H., F.W. Fisk & M. Estribi. 1983. Faunistics of Panamian Cockroaches (Blattaria). *Uttar Pradesh Journal of Zoology* **3**: 1-9.

(Accepted for publication on 19 January 1996)