

Composition and species richness of forest plants along the Albertine Rift, Africa

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The Albertine Rift is composed of a system of mountains from Lake Albert to Lake Tanganyika and harbours a high proportion of endemic species. In this area, 16 1-ha plots of 20 m × 500 m were placed in semi-evergreen forests between 770 m to 1520 m; 12 in Uganda and four in Congo. In the Ugandan plots, soil samples were taken for analyses and ground herbs (divided into pteridophytes and angiosperms), trees, climbers and epiphytes were inventoried. From the Congolese plots only data for ground herbs and trees are included. Species richness of ground herbs and trees were correlated with altitude but do not conform to simple models on Pleistocene refugia and might also be explained by environmental factors of the present. Species composition matrices calculated on the bases of presence-absence for each of the five plant groups were highly and significantly correlated and thus any of them can be used as a rough indicator of more general floristic patterns, which provides a tool for rapid assessment of species composition in other Albertine forests in the future. The floristic pattern of most plant groups were correlated with patterns in altitude, pH and cation concentrations (which were intercorrelated). Species composition has two components related to altitude: an Albertine submontane and a Congolese lowland.

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Introduction

The Albertine Rift consists of a long belt of mountains on either side of the Western Great Rift Valley extending from Lake Albert (on the border between Congo and Uganda) through parts of Burundi and Rwanda to the southern tip of Lake Tanganyika. The mountain chains of eastern Congo (including Mts. Bleu and Butumbas, the Kivu ridge) form the western flank of the Great Rift Valley and separate the Nile and Zaire basins. The Albertine Rift is noted as a hotspot in species richness and endemism for birds (Prigogine 1988; Bibby *et al.* 1992) and other animals; the most known of the latter being the mountain gorilla (*Gorilla gorilla beringei*). In a numerical analysis of species distribution of 794 plant species, Linder (1998) identified the western rift mountains as one of the four most important areas of high plant species richness in the African continent. For the Albertine Rift, about 5,800 plant species were compiled from lists and floras (Plumtre *et al.* 2003) which equals 15% of the plant species in mainland Africa. The Albertine Rift area has a complex geography including montane and submontane forests and several phytochoria (plant geographical regions according to White 1983) meet in this region. The Albertine plant species constitute 23% of of the species in the Guineo-Congolian, Afromontane and Zambesian phytochoria. A total of 567 species endemic to the Albertine Rift have been identified to date (Plumtre *et al.* 2003), some of which were discovered in the sites inventoried for the present study (Poulsen & Lock 1997; Poulsen & Nordal 1999; Poulsen *et al.* 1999; Verdcourt 1998). Due to pressure from high human population densities in their proximity, several forests in the Albertine Rift are listed as containing many highly endangered species (Plumtre *et al.* 2003).

In Central Africa, two main centres of species richness and endemism have been

identified. Present day patterns in species distribution have been interpreted to reflect the climatic history and effect of the most recent ice age and in Africa led to proposals of forest refugia: one in Cameroon and Gabon and a second near Ruwenzori-Kivu (Kingdon 1971) called the Central Refuge, which is adjacent to the Albertine Rift. This has been generally supported using present-day distribution patterns of plants (*e.g.*, Robbrecht 1996), primates (Colyn *et al.* 1991) or birds (Diamond & Hamilton 1980). In Uganda, Hamilton (1974) speculated that forest has persisted in the very southwest and near the Ruwenzori and expanded from there to colonize the forested areas of today. However, more recent investigations on palaeoecological evidence (Jolly *et al.* 1997) rejects that a forest refuge extended to the eastern flanks of the Albertine Rift, that is *in* Uganda, but do not rule out the possibility that a major refuge could have existed in E Congo. This would have acted as a source for the replacement of grassland and scrub in Uganda with medium altitude forest. However, Jolly *et al.* (1997) dispute that intact vegetation belts simply shifted along altitudinal gradients; the pollen data suggests a more complex response possibly strongly influenced by local differences in edaphic conditions and distance to potential dispersers, and that species which presently occur separated along altitudinal gradients could have been mixed in the past. Moore (1998) suggested that forests survived in patches rather than as a major block.

In this paper we first investigate if floristic patterns and species richness can be explained by factors of the present-day environment alone and we speculate if Pleistocene refugia may also have played a possible role. We test some simple hypothesis of species richness decreasing with distance from postulated refugium but simple and realistic models are not easily made. The main aim of this paper is subsequently to test if patterns of species com-

Table 1. Estimated altitude, estimated annual rainfall, and forest type (after Howard 1991 and Makana *et al.* 1998) for the 16 plots in Uganda and Congo near the Albertine Rift.

Country	Uganda												Congo (Ituri)			
Forest site	Bwindi			Kasyoha			Kibale			Budongo			Edoro		Lenda	
Plot code	BW1	BW2	BW3	KK1	KK2	KK3	KI1	KI2	KI3	BU1	BU2	BU3	ED1	ED2	LE1	LE2
Rainfall (mm)	1750	1750	1875	1375	1375	1375	1500	1500	1375	1470	1470	1270	1672	1672	1672	1672
Altitude (m)	1347	1315	1518	1325	1309	1399	1445	1379	1241	1043	1030	1011	800	800	770	770
Forest type	Mixed <i>Parinari</i>			Mixed <i>Parinari</i>			Mixed <i>Parinari</i> or <i>Cynometra</i> -dominant			Mixed <i>Khaya</i> or <i>Cynometra</i> -dominant			Mixed		<i>Gilbertiodendron</i> dominant (Mbau)	

position of different plant groups inventoried in forest plots at different sites in the Albertine Rift area reveal the same floristic pattern.

Study sites and methods

The fieldwork was conducted 1994-99 in semi-evergreen, low to mid altitude forest with annual rainfall less than 2000 mm (Tab. 1) and two annual dry seasons: most distinct in January-February; less so in July-August. Human disturbance has a long history in this region (Howard 1991; Jolly *et al.* 1997). A total of 16 1-ha plots of 20 × 500 m were established; 12 plots at four sites (Bwindi, Kasyoha, Kibale and Budongo) in Uganda and four plots at Edoro and Lenda) in the Ituri Forest, Democratic Republic of Congo (Fig. 1). The Ugandan plots were established in relatively intact forest, avoiding extensive gaps and recent disturbance, and deliberately orientated so that they crossed the steepest gradient from valley bottom to ridge top. Detailed maps of the positions of most of the Ugandan plots can be seen in Poulsen (1997). In Congo, the plots were placed in the centres of existing permanent plots of 200 × 500 m established by Hart *et al.* (Makana *et al.* 1998) with the objective to study the difference between mixed (at Edoro) and monodominant (at Lenda) forest types. The

most distant plots of the 16 plots were 386 km apart, whereas the closest were 1 km apart (distances measured between centres of plots). Forest dominance by *Cynometra alexandri* C.H.Wright was included in one site at Kibale and one site at Budongo; monodominance by

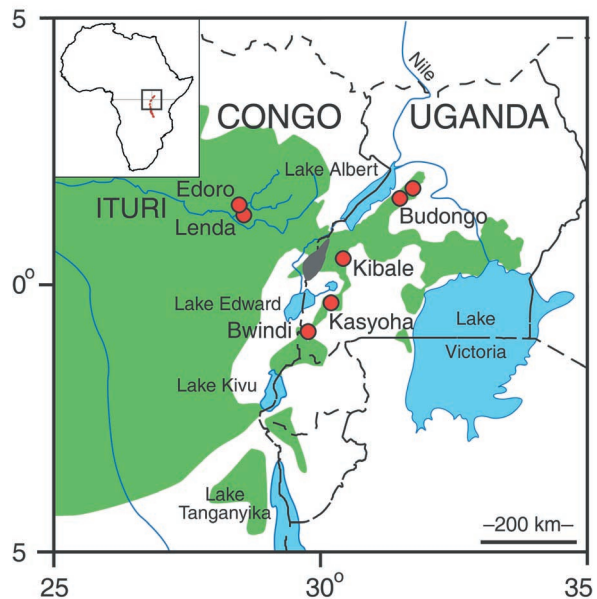


Fig. 1. The position of the study sites along the Albertine Rift, which extends south from Lake Albert via the string of lakes to Lake Tanganyika. Existing or presumed once forested areas (after Howard 1991) are shown in green shade. The Ruwenzori Mts. are in the centre of the map.

Gilbertiodendron dewevrei (De Wild.) J. Leonard – the mbau forest – was pronounced in the two Lenda plots.

Rainfall was estimated comparing the site location to the nearest isohyets in precipitation maps from the Biomass Division of the Uganda Forest Department, Uganda. A Thommen Altimeter calibrated at the nearest location of known altitude was used to read that of the plot. Slope was determined using the Suunto Clinometer. Latitude and longitude were inferred from maps.

In the Ugandan plots, a soil sample was collected in every 10 m sub-unit along each transect and five sequential samples were pooled resulting in ten samples for each transect. The five samples were collected from 15 cm deep pits and the sampling was done diagonally starting at alternate corners of each 20 m × 50 m sub plots in order to control for local variations within the transects. Air-dried samples were thoroughly mixed and passed through a 2-mm sieve and composite samples of 500 g taken for analyses in the soil science laboratory, Faculty of Agriculture, Makerere University, Kampala based on Okalebo *et al.* (1993). Soil pH was measured in water (2:2.5 H₂O) using a pH meter. Exchangeable Ca, Mg, Na and K were extracted in an excess of 1 M ammonium acetate and concentrations of Na and K determined by a flame photometer, and Ca and Mg by atomic absorption spectrophotometry. Total N was determined by the Kjeldahl method in which the soil was digested in concentrated H₂SO₄ and mixed catalyst. The digest was then distilled and titrated against standard hydrochloric acid (HCl). To determine total P, the soil was digested using a digestion mixture (conc. H₂SO₄, H₂O₂, LiSO₄ and Selenium catalyst). From the digest, total P was determined using a colorimeter. Available phosphorus (P) was determined according to Bray and Kurtz (1945). Soil particle size (physical properties) was determined by the Bouy-

oucos method (1962) using a hydrometer. Percentage loss on ignition (LOI) was determined by slowly igniting 10 g of oven dried soil samples in a muffle furnace at 550°C for 3 hours.

All individuals of ground herbs were in all 16 transects inventoried only in a 5 m × 500 m band (inside the 20 m × 500 m plots used for the other plant groups). Ground herbs are defined as plants with no secondary lignification and the leaf-bearing shoots rooted at ground level (as discussed in Poulsen & Balslev 1991; Poulsen 1996a, b). Ground herbs were divided into terrestrial pteridophytes and angiosperms, which were analysed separately.

In the Ugandan transects, trees, climbers and epiphytes were all inventoried in the complete 20 m wide band, but from the database of the big plots in Congo we extracted data for trees in 20 m × 500 m areas that overlapped with the 5 m × 500 m ground herb inventories. All trees larger than 10 cm diameter at breast height (DBH), all climbers (woody and herbaceous) larger than 1 cm diameter measured 1.3 m from the base, and all epiphytes on the trees > 10 cm DBH in the plots were enumerated and vouchered. The canopy was accessed using rope techniques. Vouchers for the Ugandan plots are deposited at the university herbaria of Makerere (MHU) and Copenhagen (C) except for the tree vouchers from Congo, which are at the herbaria in Brussels (BR) and Missouri (MO). Tree vouchers from Congo plots were not matches with those from Uganda and the combined list relied on the two teams reaching consistent identification. Only about 10 taxa were not identified to species level. Most of the ground herb and tree species are included in Poulsen (1997) and Hart *et al.* (in press). A list of the species of climbers is found in Eilu (1999).

Numerical analyses were based on similarity and distance matrices. The Jaccard index (the proportion of shared species of the total number of species found at two sites) was used as a

measure of floristic similarity between plots. Similarity matrices were computed separately for trees, terrestrial pteridophytes, angiosperm ground herbs, climbers and epiphytes (the latter two only for the 12 Ugandan plots). A matrix of log-transformed geographic distances was computed as this better reflects the rapid decline of similarity at short distances between plots than a linear relationship (Condit *et al.* 2002). Nutrient concentrations were log-transformed because a given difference in concentration is likely to be ecologically more important at low values than at high. All environmental characteristics were standardised before distance matrices were computed. For each of the environmental or soil factors (or a combination of these) Euclidian distance was used when matrices were computed.

To relate the species richness numbers of plots to distance from postulated refugia in SW Uganda, the distances were rooted in our southernmost plot at Bwindi positioned in the postulated refugia, and the other distances calculated from that zero point. Linear correlations and regression were made in the statistical package JMP.

Ordinations of transects were done using Principal Coordinate Analyses (PCoA, Legendre & Legendre 1998) on the similarity matrices converted to distances by $D = 1 - S$ (where D is the distance and S the similarity value). Correlations between pairs of similarity matrices were computed using the Mantel test (Mantel 1967). The standardized form of the Mantel test was used, which computes the Pearson correlation coefficient r between the cell values of two resemblance matrices. The statistical significance of each correlation was determined by a Monte Carlo permutation test to avoid problems related to autocorrelation and non-normal distributions of the measured variables. In all cases, 999 permutations were used, which allows testing of the statistical significance at the $p < 0.001$ level for each individual

correlation. Where both can be calculated on the same data, the Mantel test gives lower values of r than the corresponding linear Pearson's correlations in univariate cases, but the two methods generally agree on whether the correlation is statistically significant (Legendre 2000). Partial Mantel tests were performed with a third matrix of log-transformed geographical distances to assess the effect of spatial distribution of the plots (Smouse *et al.* 1986). Matrix calculation, PCoA and Mantel tests were conducted using the R-package (<http://www.fas.umontreal.ca/BIOL/Legendre/indexEnglish.html>).

Results

All 16 plots

The inventories of all 16 of the 0.25-ha plots included 204 species of ground herbs (35-74 per plot) with 110,851 individuals (5,178-9,696 per plot). Of these, the terrestrial pteridophytes comprised 63 (31%) species (6-27 per plot) and 40,363 individuals (233-7180 per plot) and the angiosperm ground herbs 141 (69%) species (22-60 per plot) and 70,488 individuals (868-7974 per plot). The 16 1-ha transect plots contained 326 species of trees in total (ranging 29-81 per plot) and 7372 individuals (328-557). The highest numbers of trees were found in the mixed forest plots at Eodoro.

In the 16 plots, species richness of trees and ground herbs were negatively correlated with altitude ($r = -0.58$, $P < 0.05$); $r = -0.81$, $P < 0.001$) whereas the species richness of terrestrial pteridophytes were positively correlated with altitude ($r = 0.71$, $P < 0.01$).

The ordination of all 16 plots produced by the PCoA analysis, based on matrices involving Jaccard similarities between plots, showed that a similar pattern appeared whether using terrestrial pteridophytes, angiosperm ground herbs or trees (Fig. 2). The ordinations all had the typical arch-shape with the Congo plots in

the left 'leg' of the arch, followed in sequence from north to south by the plots of, Budongo, Kibale, Kasyoha, and Bwindi, the latter two forming the right 'leg'. Even if the Congo plots appear in the diagram to have equal distance to the Bwindi-Kasyoha and the Budongo plots, the average percentage of shared species was twice as high (12.5%) with the latter, and thus, Budongo is floristically more similar to Ituri forest. The first axis of tree ordination was correlated with altitude ($r = 0.96$, $P < 0.001$) but not with rainfall.

The Mantel test produced high correlation between the floristic similarity matrices of the three plant groups ($r = 0.84-0.90$, $P < 0.001$). If a partial Mantel test is conducted controlling for the effect of geographical distances between the plots, the r -values decrease (0.50-0.70, $P < 0.001$).

The 12 Ugandan Plots

Soils in the Ugandan plots ranged in pH between 3.58 and 6.19 (Tab. 2), the southern samples being the most acidic. LOI ranged

from 4.15 to 11.78%, phosphorous contents from 0.09 to 0.16%, and available P from 4-30 mg/kg. The concentration of exchangeable bases (sum of Ca, K, Mg, Na) varied from 1.44 meq/100g to 26.13 meq/100g, and was mainly determined by calcium, which accounted for 44 to 72% (mean 59%) of the total base content. The sand fraction dominated across texture classes, ranging from 40 to 60% of soil weight in all transects, and averaged about 50% (Tab. 2). Many soil properties were inter-correlated: Pearson correlation coefficients among soil properties showed that pH was strongly positively correlated with the concentration of cations ($r = 0.91$) and negatively correlated with altitude (-0.61), LOI (-0.60), N (-0.47), rainfall (-0.35), and silt (-0.34).

The Ugandan plots combined contained 162 ground herb species (89,662 individuals) of which 31% were species of terrestrial pteridophytes (43% of the individuals). There were 211 species of trees (ranging 29-66 per plot) and 5747 individuals (344-557), 181 species of climbers (35-62 per plot) and 5484 individuals

Table 2. Averages of pH, Loss-on-Ignition, nitrogen, phosphorous, available phosphorous, cation concentrations, and texture measured in soils from twelve plots in Uganda (averages of 10 samples per plot).

	Bwindi			Kasyoha			Kibale			Budongo		
	BW1	BW2	BW3	KK1	KK2	KK3	KI1	KI2	KI3	BU1	BU2	BU3
pH	3.80	4.63	3.67	3.58	3.60	3.79	5.70	5.83	6.19	5.87	6.06	6.11
LOI	7.48	4.88	9.55	10.16	11.78	10.90	5.40	7.18	10.14	4.15	6.61	5.89
N (%)	0.33	0.26	0.39	0.46	0.44	0.49	0.31	0.36	0.48	0.16	0.32	0.27
P (%)	0.10	0.09	0.12	0.09	0.10	0.11	0.16	0.11	0.14	0.09	0.09	0.10
avail. P (mg/kg)	6.49	5.09	21.13	18.13	15.47	9.24	13.55	4.05	30.01	11.90	6.82	8.05
Ca (me/100g)	0.65	2.09	0.73	0.64	0.87	1.37	8.26	11.65	18.69	6.98	10.27	10.48
K (me/100g)	0.24	0.27	0.25	0.37	0.33	0.31	0.39	0.58	0.52	0.37	0.44	0.30
Mg (me/100g)	0.39	1.08	0.38	0.28	0.52	0.64	3.74	4.59	6.66	3.07	4.06	4.33
Na (me/100g)	0.15	0.15	0.12	0.17	0.15	0.18	0.15	0.17	0.26	0.21	0.21	0.20
clay (%)	18.20	32.10	18.10	16.80	18.20	24.50	28.00	25.10	19.10	24.40	28.40	21.60
silt (%)	24.80	25.50	27.80	28.70	27.20	30.70	31.30	26.50	20.80	26.70	22.00	28.80
sand (%)	57.00	43.40	54.50	54.50	54.60	44.80	40.50	49.60	59.60	48.90	50.00	49.60

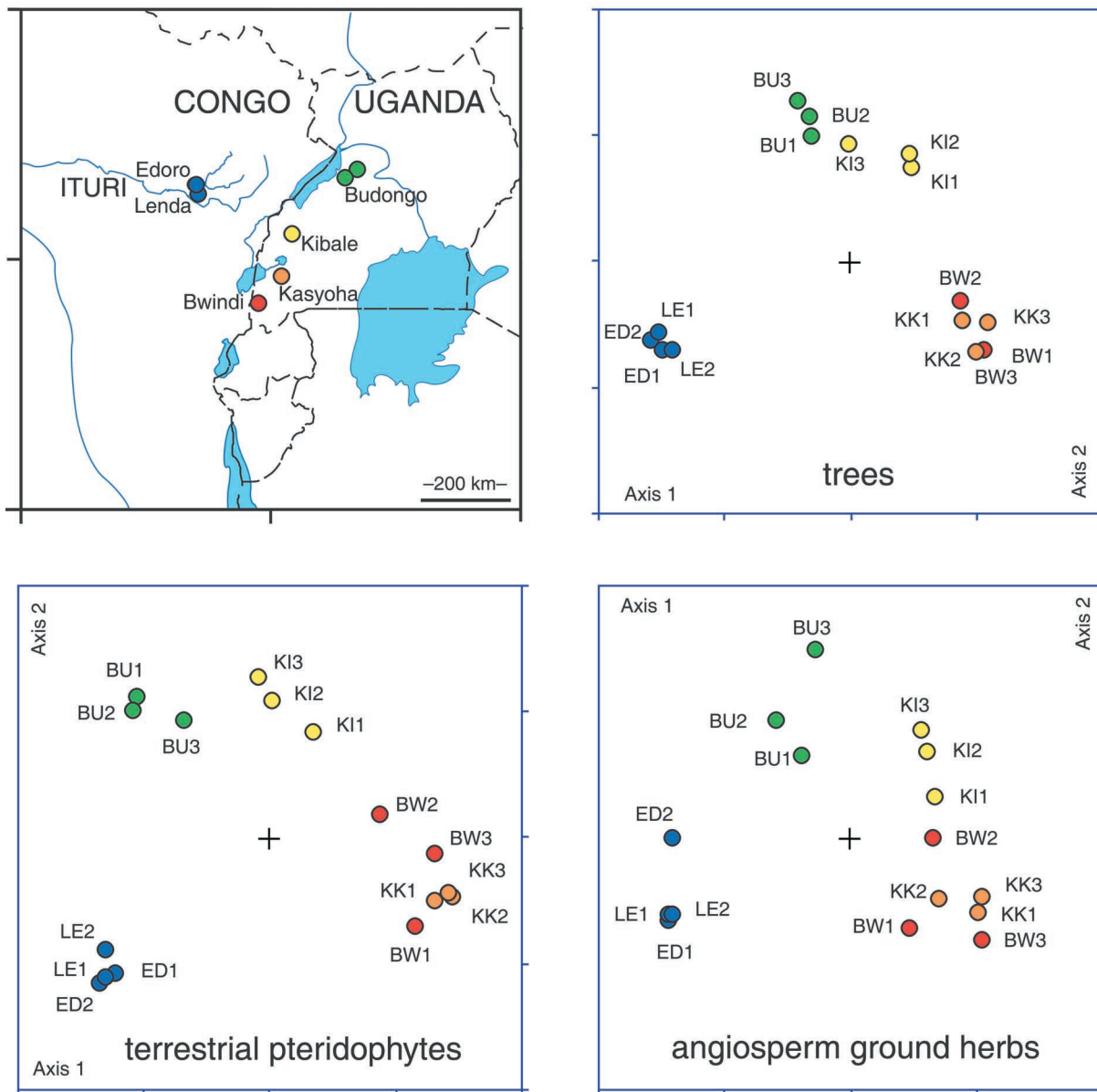


Fig. 2. Ordination diagrams (principal coordinates analysis) of 16 transects in forests in the Albertine Rift area, Africa. The Uganda sites included Bwindi (plot BW1-3), Kasyoha (plot KK1-3), Kibale (plot KI1-3), and Budongo (plot BU1-3). The sites in Ituri forest, Congo included Edoro (ED1-2) and Lenda (LE1-2). Similarity matrices are based on species composition of terrestrial pteridophytes, angiosperm ground herbs or trees. Similarities were calculated with the Jaccard index (species presence-absence data).

(155-896 per plot), and 254 species of epiphytes (46-101) and 189,027 individuals (503-88,931 per plot). These results do not exclude

the possibility of a species appearing in more than one life form category (especially between ground herbs and epiphytes) and

Table 3. Correlations obtained from Mantel Tests between similarity matrices calculated separately for five different plant groups in the 12 Ugandan plots. Significance levels are based on 999 permutations (** $P < 0.001$, ** $P < 0.01$). The correlations between floristic similarity and environmental factors were repeated in a partial Mantel Test using the log-transformed geographical distance matrix to control the effect of the spatial distribution of the plots.

	Climbers	Terrestrial pteridophytes	Angiosperm ground herbs	Epiphytes
Trees	0.86 ***	0.87 ***	0.69 ***	0.83 ***
Climbers		0.78 ***	0.75 ***	0.83 ***
Terrestrial pteridophytes			0.82 ***	0.86 ***
Angiosperm ground herbs				0.70 ***
PARTIAL LOG GEODIST				
Trees	0.62 ***	0.65 ***	0.38 **	0.57 **
Climbers		0.42 **	0.49 **	0.56 ***
Terrestrial pteridophytes			0.65 ***	0.63 ***
Angiosperm ground herbs				0.38 **

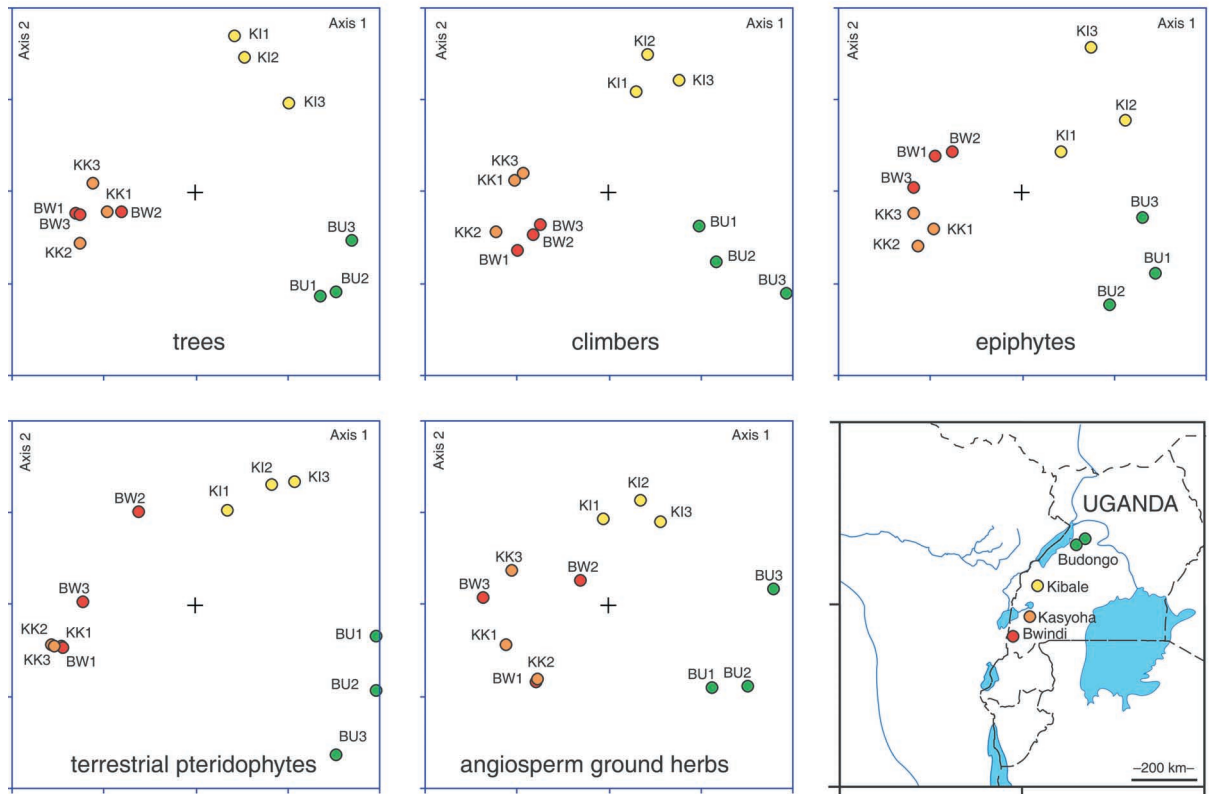


Fig. 3. Ordination diagrams (principal coordinates analysis) of 12 transects in Ugandan forests including Bwindi (plot BW1-3), Kasyoha (plot KK1-3), Kibale (plot KI1-3), and Budongo (plot BU1-3). Similarity matrices based on species composition of five plant groups: terrestrial pteridophytes, angiosperm ground herbs, trees, climbers, and epiphytes. Similarities were calculated with the Jaccard index (species presence-absence data).

Table 4. Correlations (measured with the Mantel test) between floristic similarity matrices produced separately for five different plant groups and matrices on the basis of geographical distance between plots and several individual or combined environmental factors (using Euclidean distance). The correlations between floristic similarity and environmental factors were repeated in a partial Mantel Test using the log-transformed distance matrix to exclude the effect of the spatial position of the plots. Significance levels are based on 999 permutations (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). The proportion of statistically significant correlations expected at random at the $p < 0.05$ level is one out of 20 tests, clearly lower than found here. Since the null hypothesis of the Mantel Test is one-tailed, negative correlations are replaced by dashes in the table.

	Terrestrial pteridophytes	Angiosperm ground herbs	Trees	Climbers	Epiphytes
Geographical distance	0.79 ***	0.74 ***	0.76 ***	0.75 ***	0.75 ***
Log geographical distance	0.80 ***	0.66 ***	0.79 ***	0.79 ***	0.78 ***
ENVIRONMENTAL FACTORS:					
Altitude	0.59 **	0.65 ***	0.66 ***	0.62 ***	0.49 **
Annual Rainfall	0.09 *	0.22	0.10	0.32 *	0.20
pH	0.72 ***	0.57 ***	0.65 **	0.52 ***	0.66 *
LOI	0.14	0.08	0.09	0.092	0.15
N	0.14	0.05	0.13	0.17	0.25
P	0.05	–	0.25	–	–
avail. P	–	–	0.002	0.00	0.05
Cations	0.61 ***	0.37 **	0.69 ***	0.56 ***	0.67 ***
Texture	0.04	–	–	–	–
Partial test excluding effect of log geographical distance:					
Altitude	0.27 *	0.45 **	0.42 **	0.34 *	0.11
Annual Rainfall	–	–	–	0.01	–
pH	0.59 **	0.34 **	0.44 **	0.20	0.46 **
LOI	0.02	–	–	–	0.04
N	–	–	–	–	0.11
P	–	–	0.28	–	–
avail. P	–	–	0.11	0.11	0.18
Cations	0.40 **	0.06	0.54 ***	0.31 *	0.50 ***
Texture	0.20	–	0.12	–	–

adding these numbers would be a slight overestimate of the combined species richness.

Regressions between species richness of the five plant groups in Uganda and 11 of the environmental factors were significant ($P < 0.05$) in more than one out of 20 cases. As in the 16 plots, angiosperm ground herbs were negatively and terrestrial pteridophytes positively correlated with altitude. Epiphyte richness showed a correlation with annual rainfall ($r = 0.78$) and cation concentration ($r = -0.70$). The species richness of climbers were positively correlated with clay-content $r = 0.67$). Regressions

between species numbers and distances to the SW corner of Uganda (on the assumption that this area acted as a refugium and there would be a negative relationship between species richness and distance) was significantly negatively correlated for terrestrial pteridophytes ($r = -0.75$, $P < 0.01$), epiphytes (-0.67 , $P < 0.05$) but also with annual rainfall ($r = -0.61$, $P < 0.05$), but positively correlated with angiosperm ground herbs ($r = 0.61$, $P < 0.05$).

The ordination including only the 12 Ugandan plots (which shortens the altitudinal gradient by removing the plots of the lowest alti-

tude) but include five different life form groups (Fig. 3) gave a similar pattern to that including all 16; the plots from Bwindi and Kasyoha in the south tended to mix, while the transects from Kibale and Budongo formed two separate clusters. The Budongo plots shared consistently more species with the geographically closer Kibale plots than with the plots further to the south. The first axis of tree ordination was again correlated with altitude ($r = 0.84$, $P < 0.001$) and not surprisingly also with pH ($r = -0.81$, $P < 0.01$) and cation concentration ($r = -0.63$, $P < 0.05$).

The Mantel tests of pair-wise correlations between the five plant groups were strong and significant (Tab. 3) even when controlling for the effect of geographical distance. The highest correlations were between trees and terrestrial pteridophytes (0.65, $P < 0.001$) and the lowest between ground herbs and trees or epiphytes (0.38, $P < 0.01$). The species composition matrices of all plant groups were all highly correlated with the matrix of geographical distances between the plots (Tab. 4) as well as to some of the environmental factors, especially altitude, pH, and cation concentration. The partial Mantel test conducted to exclude the geographical effect reduced the correlations and their probabilities but all three factors still remained correlated and significant at least for four of the total five plant groups.

Discussion

Species richness

Our species richness results compared to other inventories underline the known fact that Africa's forest ecosystems are relatively poor in plant species compared to other continents (Richards 1973; *e.g.*, for pteridophytes see Koronas 1993); the pooled number of tree species in all 16 1-ha transects up to 400 km apart (326) is only slightly higher than what was

found in a square plot of one hectare in lowland Ecuador (Valencia *et al.* 1994) but the richness maximum in our plots of 81 species in Congo is comparable to previous results in Africa (Whitmore 1975). Species richness of climbers in 20 m \times 50 m was about twice as high in some lowland African and Neotropical forests (Gentry 1991) and more liana species were found in one hectare on Barro Colorado Island, Panama, Putz (1984) than in our study (65 vs. our average of 51 including all climbers). Species numbers of terrestrial pteridophytes in an Amazonian lowland rainforest using exactly the same methodology (Tuomisto *et al.* 2002) were about twice as high (mean = 35, 12-46) as the present study (mean = 16, 6-26) even when the density was about half in the Neotropical study (mean = 1251, 360-2521 vs. mean = 2533, 233-7180).

As our study sites are situated in climatic conditions at the margin of what is necessary for the persistence of rain forests, it is not surprising that our species richness results are relatively low, but within the sites species richness was generally not correlated with the annual rainfall, the only exception being epiphytes. This may be due to the possibility that the available information on rainfall and seasonal variation were inaccurate, or that a longer rainfall gradient than in the present dataset is necessary to reveal such relationships. Lwanga *et al.* (1998), including three of our sites in their analyses of 12, found that species richness of terrestrial pteridophytes in Uganda was correlated with rainfall. They also included sites in drier areas of Uganda and thus sampled a longer rainfall gradient and placed emphasis on the mean number of rainy days in the wettest part of the forest, which they propose is a more sensitive indicator of average soil moisture content than total rainfall (that we used). Lwanga *et al.* (1998) also found a positive correlation with soil C/N

ratios; our results do not support that species richness of pteridophytes were correlated with any soil variable.

Species richness and the possible existence of Pleistocene refugia

Lwanga *et al.* (1998) found a weak tendency for relative species richness of ferns to decline with increasing distance from nearest (by Hamilton 1974) postulated Pleistocene refugium, more specifically, the south-western corner of Uganda (which includes the Bwindi N.P.). This model is an oversimplification, as Hamilton (1974, illustrated with a map in 1982) also speculated that trees migrated E-W from Semliki (Fig. 1, centre, just N of Ruwenzori Mts.) and continuous forest may have persisted also at the base of Ruwenzori. In any case, our regression between the plot distances based on the assumption of the simplified model had rather contrasting relationships in which terrestrial pteridophytes and epiphytes conform by having a negative correlation; angiosperm ground herbs showed the complete opposite pattern. It is in the first place perhaps not appropriate to use terrestrial pteridophytes as indicators of forest refugia since their spores are very well dispersed (Smith 1972; Conant 1978). The negative correlations by richness of epiphytes or terrestrial pteridophytes with distance from postulated refugium could equally well be explained by rainfall. On the other hand, it is not surprising if present-day rainfall distribution would be correlated to those of proposed forest refugia since present-day topographic patterns, which are to a large extent determining rainfall patterns, probably also contributed to those of the past (Hamilton 1992). The decreasing fern richness in plots further north it is also associated with decreasing elevation, which also conforms with the general pattern that pteridophyte species richness is lower in the lowlands than at higher altitude (Moran 1995).

Based on more recent evidence (Jolly *et al.* 1997) it is highly unlikely that the Bwindi area acted as the source of species to colonize the lower altitudes in Uganda (including Budongo) but species could have dispersed from the western flank of the Albertine Rift to Bwindi and then followed the proposed route. The species richness decline of angiosperm ground herbs and trees from the Congo to the Budongo plots clearly suggest there may have been a dispersal that way as thought by Hamilton (1974, 1982), and floristic similarities clearly show that the plots from Budongo share more species with the Congo plots than any plots in Uganda. Budongo is essentially just an outlier at the rim of the Guineo-Congolese rain forest (White 1983). If one must speculate on refugia, it is thus probable that there were both a highland and a lowland source involved and that the process was more complex than a simple invasion. In the mapping of bird distributions in the area, Bibby *et al.* (1992) recognizes the East Congo Lowland and the Albertine Rift Mts as two distinct centres of bird endemism. Thus, if any forest recolonization took place in Uganda it is more likely it had two sources – even if plant distribution along altitudinal gradients 10 000 years ago may have been rather different or much more compressed than at present (Jolly *et al.* 1997). We do not interpret our data to support the existence of two distinct refugia but rather that there are floristic differences that depend at least on altitude. Poulsen and Lock (1999) have already discussed this, based on the distribution of just 16 species of gingers in 13 of our present plots, and the much larger dataset included in the present paper corroborates this. This conclusion conforms with the early thoughts of Hamilton (1974).

Floristic composition

Previous studies in the species rich rain forests of Peruvian Amazon by Tuomisto *et al.* (1995, 2003), Ruokolainen *et al.* (1997), Ruokolainen

and Tuomisto (1998) demonstrated that different plant groups inventoried in a series of plots can produce similar floristic patterns. This was shown by running pair-wise Mantel tests between the species composition of pteridophytes, members of the family Melastomataceae and trees in plots at the same regional scale as the present study.

The positive and significant correlations between the species composition of the five different plant groups indicate that it is possible to get insight to the general pattern in the floristic variation based on a subset of species. In this case, it would be easier to study plants that do not involve tedious or potentially dangerous climbing, like terrestrial pteridophytes (as suggested by Ruokolainen *et al.* 1997). As mentioned above, one attempt has already been made to study forests in Uganda based on rapid assessment of ferns (Lwanga 1998) though no correlations with other plant groups were made.

Further subdivision of the angiosperm ground herbs may be a promising next step in order to identify if one particularly easily identifiable family may serve as a potential indicator of the overall pattern. This becomes even more crucial for gaining an understanding of the complex biogeography in the endemic-rich Albertine Rift forests, which are under increasing pressure from humans.

Our species composition data are clearly highly correlated with geographical distance mainly because the plots follow a S-N gradient that is also closely related with altitude. Hamilton (1974) noted that there is a clear relationship between altitude and distribution of the dominant tree species in Uganda, so that *Parinari* forest is above 1400 m (which we have as a dominant component of our plots at Bwindi and Kasyoha) and *Cynometra-Celtis* (700-1200 m). *Cynometra alexandri* was especially abundant in one plot in Kibale, one in Budongo, and the Egoro plots (Tab.1). Our data cer-

tainly conform to the tree dominance observations by Hamilton (1974) even though, in our ordination diagrams, plots dominated by *Cynometra alexandri* still tended to stay in their site group rather than clustering with other plots with dominance by the same tree species.

Floristic composition and environmental factors

When the effect of geographical difference between plots is excluded, some environmental characteristics remain positively and significantly correlated which implies that a large part of the variation in our data can still be explained by factors of the present-day environment. Hamilton (1974) observed also that species typical of the *Parinari* Zone occurred only at lower altitude in the highest rainfall area, but even if there is a tendency for our rainfall estimates to correlate with altitude, they were not significant. Possibly our rainfall estimates are not sufficiently accurate. It is worth bearing in mind that the rainfall pattern in Uganda is very patchy and the length of the dry period has a major effect on the vegetation (Hamilton 1984).

The Neotropical studies (Tuomisto *et al.* 1995, 2003; Ruokolainen *et al.* 1997; Ruokolainen & Tuomisto 1998) also demonstrated that floristic patterns reflected edaphic conditions. Vormisto *et al.* (2000), at the local scale of one transect of 20 m × 500 m, showed that the floristic composition of four plant groups were correlated with each other and with edaphic characteristics. Thus, result of the present African study does not come as a surprise, and that the matrix of cation concentrations is significantly correlated with most of the species composition matrices, is in accordance with the Neotropical studies, where, similar to our result, pH was also found to be important in one case (Ruokolainen *et al.* 1997). For the pioneer study by Hall & Swaine (1976) on trees in Ghana, the concentration of cations (which

was correlated with rainfall and pH) was also mentioned to correlate best with the first axis of their ordination. In contrast with the Neotropical studies, we did not find evidence supporting that texture is an important factor. The correlation values of our Mantel tests are comparable to those found in the Neotropical studies but somewhat lower than found at the same regional scale most likely due to the mosaic structure of the Amazonian environment, as opposed to our plots which followed a strong gradient.

Conclusion

Any of the five studied plant groups of ground herbs (divided into pteridophyte and angiosperms), trees, climbers or epiphytes can be used as a rough indicator of more general floristic patterns. This is demonstrated here for the first time on data from the Old World Tropics and for the first time when including angiosperm ground herbs, climbers and epiphytes. The floristic patterns were correlated with altitude, pH and cation concentrations and these results suggest that deterministic processes of the present-day environment to a large extent can explain the distribution of species in forests of the Albertine Rift even if historical factors cannot be ruled out. The practical implication of our results is that it may be possible to gain understanding of the overall pattern in the floristic variation based on a small sub-sample including conveniently only those plants, which are easy to study. Species richness patterns for some plant groups correlated with altitude and species composition has two components which are related to altitude: an Albertine submontane and a Congolese lowland and there is a gradual transition in species composition along the gradient covered.

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