

Relationships between native tree species and soil properties in the indigenous forest fragments of the Eastern Arc Mountains of the Taita Hills, Kenya

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Abstract The relationship between soil properties and spatial distribution of native woody species was studied in three Taita Hills forest fragments which, although degraded, are ranked among 34 biodiversity hotspots of the world due to their high biodiversity of both plant and animal species. This relationship was assessed by using Spearman correlation and principal component analyses (PCA). The results of these analyses should be useful in instituting forest restoration programs that are crucial for the forests. Both the soil and vegetation studied were sampled from 17 subplots in the natural forest fragments of Ngangao (120 ha), Chawia (86 ha) and Mbololo (185 ha). The soil variables measured were: pH, texture, soil nutrients of C, N, Ca, P, K, Mg and Na. In total 36 native tree species from 13 families were identified from the three forest fragments. Ordination results show that axis 1 accounted for 35% and axis 2 for 25% of the total variation in species composition, indicating that the structure of vegetation is related to two major environmental gradients. The correlation analyses of species and soil properties showed that Na and clay particles were the most important determinants of species distribution; pH and soil variables such as C, N, Ca and P also played minor roles. Unexpectedly, some species (e.g. *Psychotria petiti*) showed positive relationships with Na attributed to possible substitution for K. Relationships with P were both positive (e.g. *Craibia zimmermannii*) and negative (e.g. *Albizia gummifera*) with some species, attributable to pH levels. An ANOVA for soil variables showed that there were differences in the Ca content in Mbololo (due to the parent material) and P in Ngangao where a special relationship was observed between some of the species. The presence of gaps accounted for the distribution of seedlings but not for the saplings, whose distribution responded more to factors similar to those to which mature trees respond. Soil-species relationships that were established may be utilized along with soil analyses when choosing native species for restoration.

Key words Eastern Arc Mountains forests, principal component analysis, soil variables, native woody species

1 Introduction

Plants differ in their requirements and tolerance to several soil variables such as nutrients, salinity and moisture conditions. It is important to understand the ecological relationship between soil variables and tree species in order to plan and execute a successful forest restoration program for fragmented forests such as those of the Taita Hills, Kenya. The forests of the Eastern Arc Mountains (EAM) of the Taita Hills in East Africa are recognized internationally for their

biodiversity and are regarded as some of the 34 key biodiversity hotspots in the world (Myers et al., 2000; Conservation International, 2005). Nonetheless, they are under major threat from disturbances due to anthropogenic activities. The effects of disturbance as an environmental variable have been studied in these forests (Bytebier, 2001; Pellikka et al., 2009; Omoro et al., 2010) and found to have led to the alterations in the composition and structure of woody species. Findings which are similar to observations by other investigators (Echeverría et al., 2007; Muhanguzi et al., 2007; Rixen et al., 2007) established that forest dis-

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turbances not only impacted species composition and structures but also caused the disappearance of susceptible species (Onaindia et al., 2004), while in some cases the disturbances led to the improvement of species mixes (Fox, 1979; Hobbs and Huenneke, 1992; Rogers, 1996). Other environmental factors known to affect species composition and distribution include topography and climatic conditions (Zhang et al, 2006; Peter and Marion, 2008), soil moisture and salinity (Swain, 1996; Xu, 2008).

The relationship between soil and woody vegetation is complex, whereby soil provides physical support for the vegetation in addition to nutrition that affords growth. Vegetation, in turn, contributes to the pool of soil nutrients through nutrient cycling. Studies have defined this important aspect of vegetation-soil relationships as a “nutrient pump” (Evans, 1992; van Noordwijk and Purnomosidhi, 1995) because the trees extract nutrients from greater soil depths to use and eventually release the same nutrients through litter fall and decay. This nutrient cycling phenomenon is particularly important in the tropics because it maintains the ecosystem which inherently suffers from low soil fertility (Sanchez and Palm, 1996; Schulte and Ruhayat, 1998). Several of the soil-vegetation relationships that have been studied have shown varied results. Whereas some results have clearly shown how the spatial distribution of species is related to climatic conditions on a local and global scale (Woodward and Williams, 1987), those which show relationships with soil variables have inevitably been on a smaller scale (Swaine, 1996). Xu et al. (2008) for instance studied this connection and found a relationship between vegetation and soil moisture along different topographic positions. Other studies conducted in saline conditions (Ukpong and Areola, 1995; Jafari et al., 2003) showed cases of these relationships with specific vegetation types, results which can be attributed to the adaptive mechanism of those particular plants. Specific studies on the relationships between soil nutrients and spatial distribution of tree species include those by van Breemen et al. (1997) who observed a relationship between specific species with calcium and magnesium, attributed to the effect of parent material. Vincent and Meguro (2008) showed a relationship between species abundance and soil nutrients in their study of different ecosystems. With regard to specific studies on soil nutrients and vegetations, nutrient limitations were shown to affect plant structure (Grime et al., 1997), species composition (Koerselman and Meuleman, 1996) and the distribution of species.

In the tropics however, some of the soil-vegetation relationships analyzed include those by Ruggiero et al., (2002) who found distinct differences in the distribution of vegetation types and specific soil vari-

ables. Ukpong (1995) showed the effects of specific soil variables on the distributions of mangrove communities. In some studies, instances have been noted where certain vegetation types have been perceived to indicate soil quality such as fertility (Habarurema and Steiner, 1997) and responses to other environmental conditions such as rainfall (Swaine, 1996). Despite these isolated relationships, known cases where direct correlations exist between vegetation and specific soil nutrients are few; for instance, Hironka et al. (1991) in their review give an account of how difficult it is to generalize soil-vegetation relationships since both are a product of the same environmental variables.

In this study area, no evaluations have been made to assess whether and to what extent changes in species composition correspond to specific soil variables. Such information is in fact still sparse for many tropical regions (John et al. 2007), even though the information is crucial for planning successful restoration activities. For the conservation, sustainable management and possible conversion of exotic tree plantations into natural forests, knowledge about how the distribution and regeneration of native tree species are related to soil properties is needed (The Taita Biodiversity Conservation Project, 2004; Omoro et al., 2010). A major goal of this study was to understand the relationship between natural woody vegetation and soil as an environmental variable for the forests of the Taita Hills. The information obtained could increase the effectiveness of the current restoration programs in these forests where exotics are being replaced by native tree species. The presence of exotic species is one of the reasons attributed to the degradation of the forests (Rogo and Oguge, 2000). Furthermore, the restoration would be more efficient if the tree species matched the soil variables of the sites. The specific objectives of our investigation were to determine how the native woody species in these natural forests are distributed in relation to soil texture, soil pH and nutrients and to determine whether native tree seedling regeneration is related to light conditions. The spatial distribution was assessed for the following soil variables: carbon (C), nitrogen (N), potassium (K), magnesium (Mg), sodium (Na), exchangeable calcium (Ca), phosphorus (P), pH and soil texture. The hypothesis for the study is that the distribution of native woody species within the natural forest stands depends on the physical and chemical characteristics of the soil.

2 Materials and methods

2.1 Study area

This study was conducted in three fragments of natu-

ral Eastern Arc Mountains (EAM) forests in the Taita Hills, south-east Kenya ($3^{\circ}25'S$, $38^{\circ}20'E$). The Taita Hills form the northernmost part of the EAM eco-region. A general description of the geography of the Taita Hills is given by Salminen (2004) while the relative structure and composition of the vegetation has been described by Beentje (1988) and Wilder et al. (1998). The three forest fragments included in this study (Fig. 1) were Ngangao, Chawia and Mbololo, all receiving about 1100 mm rainfall annually and found between 1450 and 1900 m elevation (Pellikka et al., 2009).

The Ngangao forest fragment is about 120 ha in size and the following native woody species are commonly found: *Tabernaemontana stapfiana*, *Macaranga conglomerata*, *Albizia gummifera*, *Phoenix reclinata* Jacq., *Syzygium guineense*, *Maesa lanceolata* Forssk. and *Cola greenwayi*. Surrounding this natural forest remnant are exotic plantations of *Eucalyptus saligna* Sm., *Pinus patula* Schiede ex Schlechtendal and *Cupressus lusitanica* Mill. The most common indigenous

tree species in the Mbololo forest fragment, the largest of the three fragments covering an area of 185 ha, are *T. stapfiana*, *A. gummifera*, *P. reclinata*, *Newtonia buchananii* and *Strombosia scheffleri*. It also contains exotic plantations of *E. saligna*, *P. patula* and *C. lusitanica*, each covering more than 5 ha. The Chawia remnant (86 ha) mostly has the following native tree species: *T. stapfiana*, *A. gummifera*, *P. reclinata*, *M. conglomerata* in addition to exotic plantations of *C. lusitanica* (0.5 ha), *E. saligna* (6 ha) and *P. patula* (1 ha) within the fragment. Of this group, Mbololo is considered to be the least degraded indigenous forest, while Chawia as the most degraded and Ngangao at an intermediate level (Wilder et al., 1998; Rogers et al., 2008; Omoro et al., 2010). The soils in these forests are generally classified as Cambisols (FAO, 1990) with local variations. The soils in Ngangao are described as complex and well drained humic Cambisols; in Chawia, the soils are described as well drained chromic Cambisols with friable clays and calcic Cambisols; while in Mbololo, the soils are described as

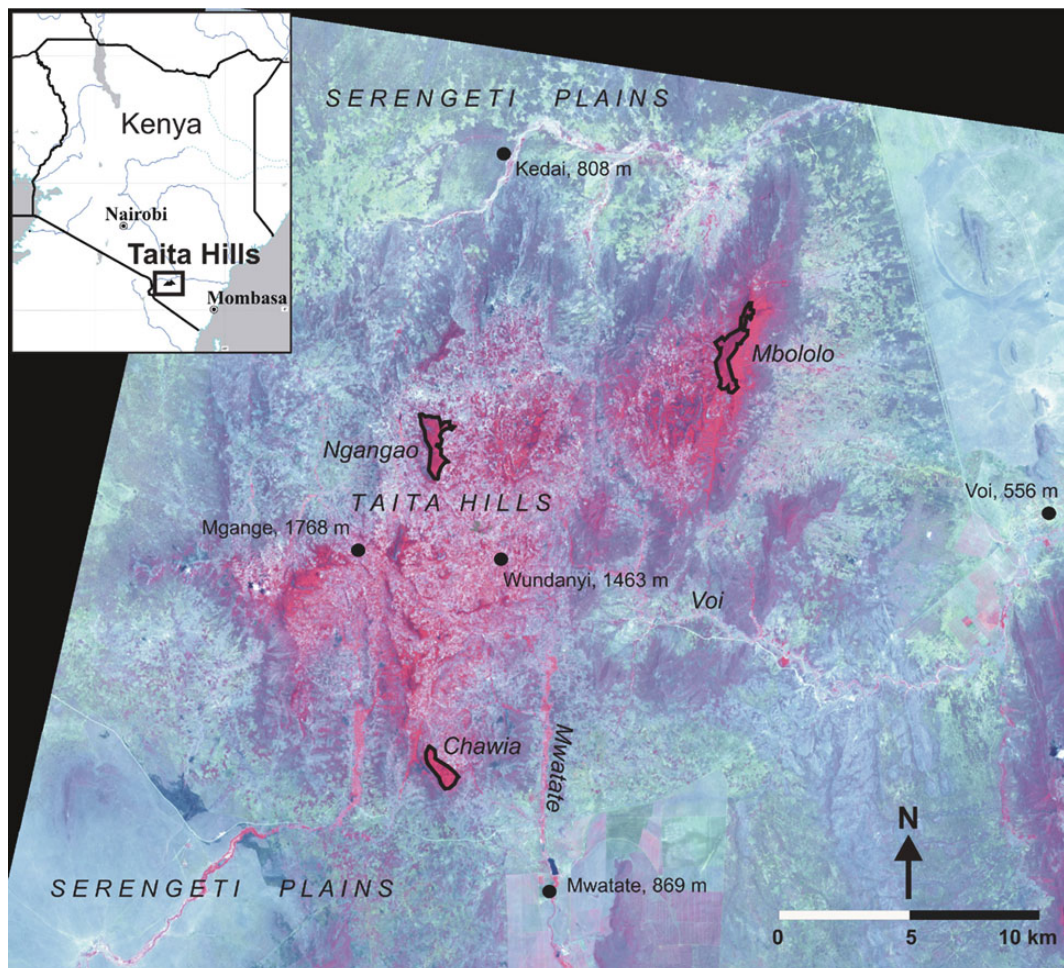


Fig. 1 Location of the three study forests (Ngangao, Chawia and Mbololo) in the Taita Hills, S.E. Kenya

complex and well drained and moderately calcareous in some areas (Jaetzold and Schmidt, 1983).

2.2 Study plots

The study was carried out in 17 subplots located in the three indigenous forest fragments and distributed as follows: 5 in Ngangao, 4 in Chawia and 8 in Mbololo; the number of subplots are in proportion to the area of the forest (Figs. 2–4). In the case of Ngangao and Chawia forests, the subplots were selected from the existing network of Forest Health Monitoring (FHM) plots (Madoffe et al. 2006; USDA Forest Service, 2007; Rogers et al. 2008). These FHM plots were established in 2000. In the case of the Mbololo forest, no such network of FHM plots exists and therefore plots of similar design were randomly established from where the soil and vegetation data were collected.

Each FHM plot consists of four circular subplots:

a central subplot (subplot 1) surrounded by three subplots formed in the shape of an inverted Y (Fig. 5). Each subplot is 7.32 m in diameter (0.017 ha in area) and the center of the three surrounding subplots are located at 36.6 m distance from the center of subplot 1. In the Ngangao and Chawia forests, two FHM plots located in the indigenous forests were chosen at random from 11 and 6 possible plots, respectively; from each plot, subplots 1 and a second one was also chosen at random out of the four subplots in a cluster constituting a plot for vegetation measurement and soil sampling. In the case of one of the FHM plots in Ngangao, a third subplot was sampled in addition to subplots 1 and 2 unlike in Chawia where only two subplots were sampled from each plot. In the case of the Mbololo forest, four plots were laid out based on the FMH protocol and eight subplots were used for sampling both the vegetation and soil data. The number of both plots and subplots sampled were relatively higher than in either the Ngangao or Chawia forests

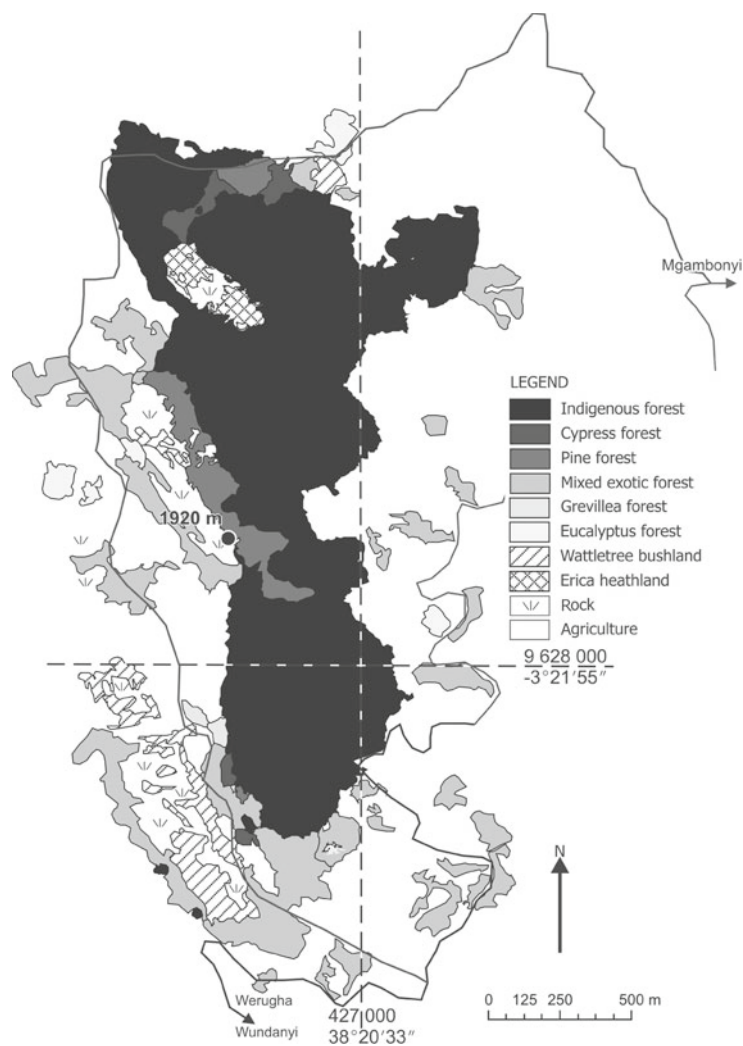


Fig. 2 Forest stands within the Ngangao fragment

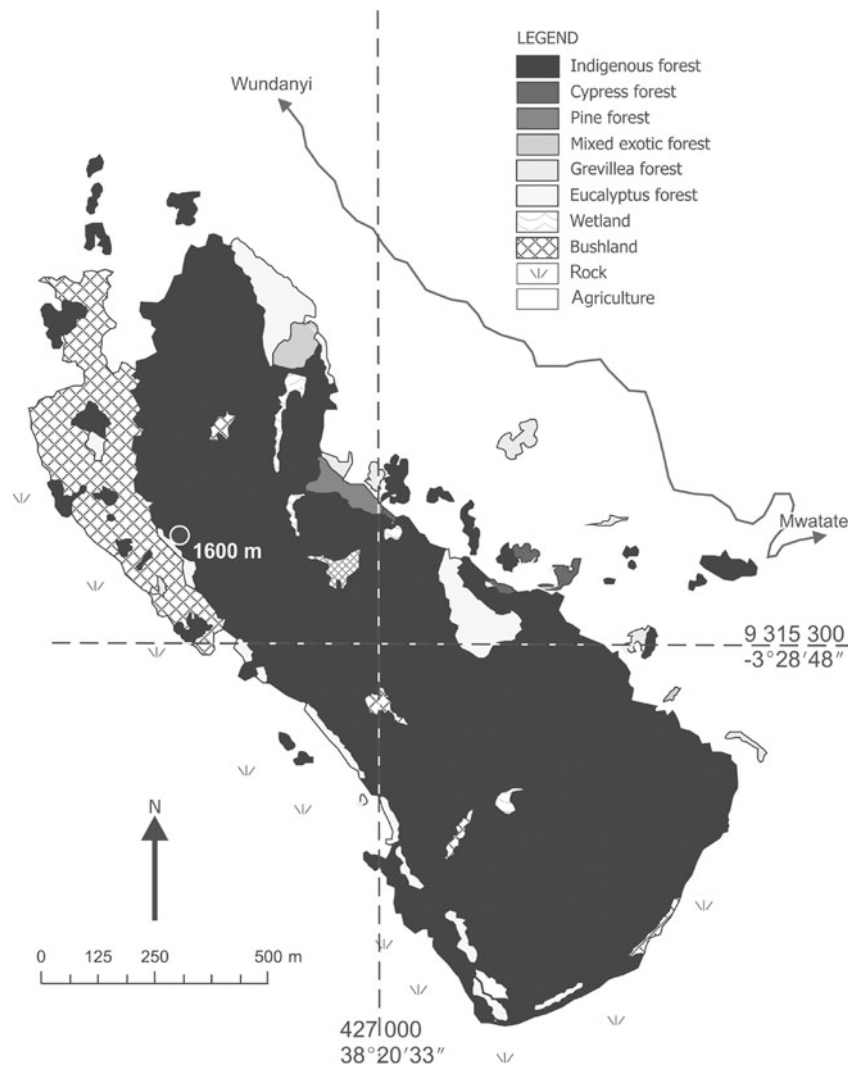


Fig. 3 Forest stands within the Chawia fragment

because the Mbololo forest is larger in size than the other two forests. Each of the subplots was equilaterally located from each center subplot 1 at a distance of 36.6 m.

2.3 Tree inventory and measurements

At each subplot all tree species were enumerated and recorded by species and size class: individual plants with diameter at breast height (DBH) > 5 cm and height > 1.3 m were classified as trees, individuals with a DBH < 5 cm but height > 1.3 m were classified as saplings and individuals with height < 1.3 m were classified as seedlings. Identification of indigenous species was accomplished by a local para-taxonomist and by use of a field instruction manual (USDA Forest Service, 2007). The botanical names are based on the African Plants Database (2009).

2.4 Soil sampling and analyses

Disturbed soil samples were collected from each of the 17 subplots using 20-cm³ volume soil augers for analysis of basic chemical and physical soil properties from soil depths 0–20, 20–50 and 50–100 cm. The main physical soil analyses were carried out for particle size distribution from which the soil texture was determined. The samples were analyzed at the Department of Soil Science, University of Nairobi of Kenya as follows: soil particle size analysis was carried out by the hydrometer method (Bouyoucos, 1962); pH (in water) using a pH-electrode (Black et al., 1965); total nitrogen (N) was determined by the modified Kjeldahl method (Bremner, 1965); total organic carbon (C) was determined by the Walkley-Black method (Walkley and Black, 1934); and exchangeable calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) were extracted by leaching through the use of 1 mol-

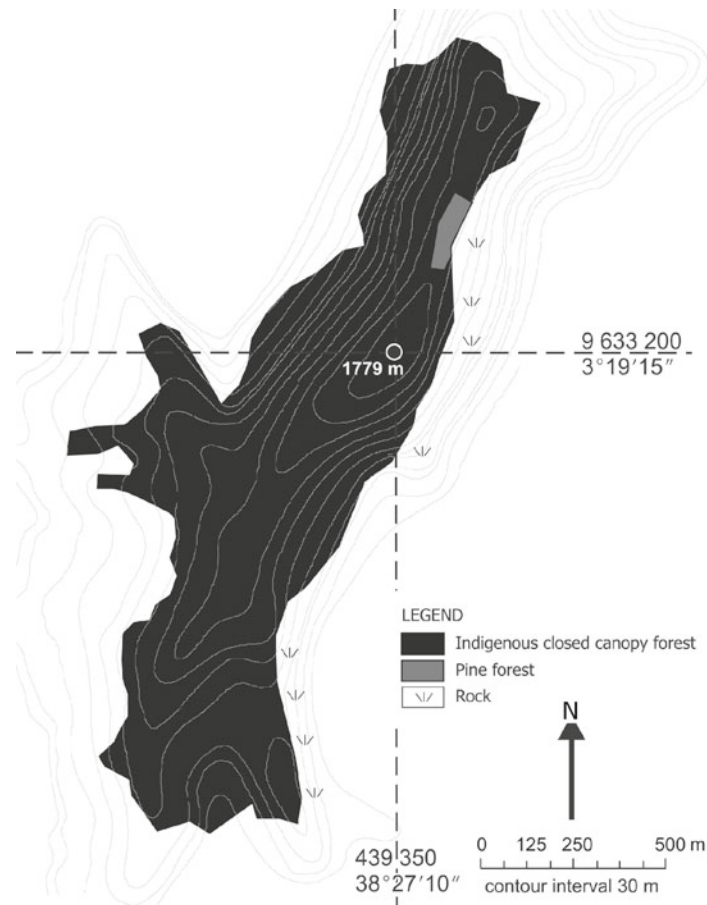


Fig. 4 Delineation of the Mbololo fragment

L^{-1} ammonium acetate. The available phosphorus (P) was extracted by double acid using $0.05 \text{ mol}\cdot\text{L}^{-1}$ HCl in $0.025 \text{ mol}\cdot\text{L}^{-1}$ H_2SO_4 and estimated by a calometric method. Details for all the analyses carried out are described in the Soil Analyses Manual (Okalebo et al., 2002).

2.5 Data analyses

The relationships between the composition and distribution of native tree species and soil properties were examined using ordination methods (Lepš and Šmilauer, 2005). Preliminary analysis of the data using detrended correspondence analysis (DCA) indicated that ordination methods based on linear responses were appropriate (Lepš and Šmilauer, 2005). Therefore, the ordination methods used were principal component analysis (PCA) to explore relationships and redundancy analysis (RDA) to eliminate species variation using CANOCO 4.52 in a Windows program. Ordination and correlation analyses for vegetation distribution were carried out for the entire soil depth of 0–100 cm after exploratory analyses showed

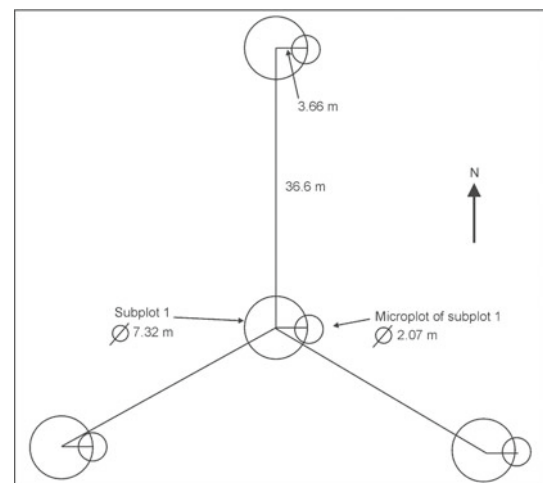


Fig. 5 Plot layout (Source: USDA Forest Service, 2007)

that the distribution of the vegetation was not different at any of the three depths studied.

In order to evaluate variations in species composition at different spatial scales (between area, plot and subplots), a series of RDAs were performed to partition the variances which was made possible by the

hierarchical structure of the samples. This partitioning was necessary because of the hierarchical structure of the sampling design. The RDA partition of the variances was accomplished as follows: the proportion of variance likely to arise from the forest sites was assessed using dummy variables which identified the areas as explanatory variables (“environmental variables” in Canoco terminology). The variance from the plot cluster level was assessed using dummy variables to identify the plot cluster as explanatory variables; and to exclude the variation from the area level, dummy variables identifying the forest areas were used as covariates (“covariable” in Canoco). Finally, the variances likely to arise from the subplot level were assessed by using dummy variables identifying the subplots as explanatory variables and dummy variables identifying forest area and plot clusters as covariates.

To evaluate the structure and spatial distributions of species compositions in the 17 subplots, a PCA ordination method was first applied. To avoid the adverse effect of rare species within the data (Jongman et al., 1987), we excluded species that occurred only once in a subplot in the entire data set. The analysis of the importance of soil properties in determining the structure, spatial distribution and species composition was based on examining their correlations with the PCA axes based on the vegetation data. Additionally, an RDA was conducted with the soil variables as the explanatory variables (“environmental variables” in Canoco terminology) to confirm whether the patterns revealed by PCA were actually contributed by the soil variables.

Spearman correlation analysis was further used to examine the relationships between species and individual soil properties, while the differences in soil properties between the forest sites were determined by a one-way analysis of variance (ANOVA) after a natural logarithmic transformation of the soil data to eliminate skewing. The statistical analyses for the ANOVA were carried out by SPSS (2007) for Windows, version 16. Tukey’s test was used to test which forest areas were significantly ($p < 0.05$) different from other areas.

To analyze the spatial distribution of seedlings and sapling species, the PCA scores obtained from the ordination analyses of the mature trees data were used in RDAs (one for each group) to test if seedlings and saplings would respond to the same environmental gradients as the mature trees. An additional factor, gaps in the mature tree layer, which was postulated to have some effects on seedling distribution, was also analyzed using total basal area (BA, m²) of the mature tree layer also as an environmental variable in an RDA for seedling densities. We assumed that a smaller BA would indicate a more likely appearance of gaps, even

though we recognized that the spatial distribution of the trees also may have some effect.

3 Results

3.1 Vegetation

The variance partitioning attributed to hierarchical levels showed that forest area accounted for 21% of total variation in species composition ($p = 0.002$), plot clusters accounted for 25% ($p = 0.004$) and subplot accounted for 12% ($p = 0.538$). This showed that there was as much variation in species composition within forest area as there was between them. Variation in species composition occurred at spatial scales greater than 40–50 m; and yet the maximum distance between subplots within a plot cluster was 36.6 m. In total, 36 species from 13 families were identified, but only 17 species appeared more than once (a minimum of two) in a subplot (Table 1). The two species commonly occurring in all the three forest remnants were *T. stapfiana* and *S. guineense*. A comparison between forest areas showed that Mbololo had the largest number of species and in higher frequencies while Chawia site had the least number of species.

3.2 Soil properties

The mean values of various soil properties for the 50–100 cm layer are shown in Table 2; other layers of 0–20 and 20–50 cm showed that there were no significant differences between the soil variables. For the ordination analyses, the entire profile depth of 0–100 cm was considered. Soil carbon and nitrogen contents were highest in Ngangao, although the differences in the contents of both elements between Ngangao and Chawia were not significant. Mbololo had the lowest carbon content of the three areas. Similarly, K contents were highest in Ngangao, properties which were significantly different from those in Mbololo but not in Chawia. Available P content in the Ngangao soils was significantly higher than that at Mbololo but not at the Chawia site. Mbololo soils on the other hand had higher Ca content than the other two sites; however, the calcium contents between Ngangao and Chawia were not significantly different. There were no significant differences in the levels of Na measured from the soils of the three forests.

3.3 Species-soil relationships

The first two principal components (ordination axes)

Table 1 Frequency of occurrence of tree species (%) in plots of the different study sites of Ngangao, Chawia and Mbololo

Family	Species appearing more than once	Abbreviation	Ngangao (n* = 5)	Chawia (n* = 4)	Mbololo (n* = 8)
Apocynaceae	<i>Pleiocarpa pycnatha</i> K. Schum.	Ple	0	0	38
Apocynaceae	<i>Tabernaemontana stapfiana</i> Britten	Tub	80	100	50
Araliaceae	<i>Polyscias stuhlmannii</i> Harms	Polst	60	0	13
Eurphobiaceae	<i>Macaranga conglomerate</i> Brenan	Mac	80	0	38
Flacourtiaceae	<i>Dasylepsis integra</i> Warb.	Das	40	0	0
Guttiferae	<i>Garcinia volkensii</i> Engl.	Gar	20	0	63
Leguminosae	<i>Albizia gummifera</i> (J. F. Gmel.) C. A. Sm.	Alb	0	75	0
Leguminosae	<i>Newtonia buchananii</i> (Baker f.) G.C.C.Gilbert & Boutique	New	40	0	75
Leguminosae	<i>Craibia zimmermannii</i> (Harms) Dunn	Cra	80	0	88
Myrtaceae	<i>Syzygium guineense</i> (Willd.) DC.	Syz	60	25	50
Olacaceae	<i>Strombosia scheffleri</i> Engl.	Str	40	0	100
Rubiaceae	<i>Coffea fadenii</i> Bridson	Cof	40	0	50
Rubiaceae	<i>Psychotria petiti</i> Verdc.	Ppet	20	0	75
Sapotaceae	<i>Aningeria adolfi-friedericii</i> (Engl.) Robyns & G.C.C.Gilbert	Ani	20	0	38
Sterculiaceae	<i>Cola greenwayi</i> Brenan	Col	20	0	38
Loganiaceae	<i>Nuxia congesta</i> Fresen	Nux	0	0	25
Rutaceae	<i>Teclea trichocarpa</i> (Engl.) Engl.	Tec	0	0	38

Note: n* denotes number of plots sampled at each forest site.

Table 2 Mean, maximum (Max) and minimum (Min) values for soil properties of the study sites of Ngangao, Chawia and Mbololo forests

Property	Ngangao			Chawia			Mbololo		
	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
C (%)	13.2 ^a	17.1	0.7	2.8 ^a	9.1	0.9	1.1 ^b	10.0	0.1
N (%)	1.1 ^a	1.7	0.1	0.2 ^a	0.7	0	0.1 ^b	0.8	0
K (cmol·kg ⁻¹)	0.7 ^a	1.0	0.3	0.4 ^a	0.8	0	0.04 ^b	1.3	0
Na (cmol·kg ⁻¹)	0.19	0.5	0.01	0.1	0.5	0	0.05	0.6	0
Ca (cmol·kg ⁻¹)	1.9 ^b	5.8	0.3	1.2 ^b	3.0	0.4	2.5 ^a	7.0	0.8
Mg (cmol·kg ⁻¹)	1.2	2.7	0.3	0.6 ^b	1.8	0.2	0.7 ^{ab}	3.1	0.2
P (mg·kg ⁻¹)	4.0 ^a	26.3	0.4	2.2 ^{ab}	9.5	0	0.7 ^b	19.3	0
pH	4.1	5.0	3.1	4.0	4.9	3.1	4.2	5.3	3.1
Sand (%)	67.6 ^a	85.0	45.0	51.9 ^c	75.0	23.0	60.6 ^b	84.0	22.0
Silt (%)	12.3 ^b	29.9	1.9	15.8 ^a	35.9	1.99	16.4 ^a	33.1	8.0
Clay (%)	17.2 ^b	40.9	4.0	29.9 ^a	46.1	11.0	18.3 ^b	56.3	1.9

Note: means followed by a different letter superscript denote significant differences between sites by Tukey's test ($p < 0.05$).

jointly explained 60% of the total variation in species composition. Axis 1 accounted for 35% of total variation and axis 2 for 25%, indicating that the structure of vegetation is related to two major environmental gradients. The PCA ordination of species (Fig. 6A) showed that *P. pycnatha* and *S. scheffleri* correlated positively with both the first and the second axes; *P. petiti*, *C. fadenii*, *C. zimmermannii* and *A. adolfi-friedericii* all had positive correlations with the first axis; *S. guineense*, *C. greenwayi*, *T. trichocarpa*, *G. volkensii*, *N. buchananii* and *N. congesta*, correlated

with the second axis. *P. stuhlmannii* was weakly positively correlated with the second axis. The other species, i.e., *T. stapfiana*, *D. integra*, *A. gummifera* and *M. conglomerata* were all negatively correlated with both axes 1 and 2. The forest site centroids (Fig. 6B) clearly show that at the Mbololo site, the species composition is different from the other two forest sites. Axis 1 correlated positively with Na and pH but negatively with C and nutrient concentrations; the second axis correlated positively with silt and pH but negatively with clay particles, C, N and base cation (Ca, K,

Table 3 The intra-set correlations of environmental variables for the four axes of the PCA

Environmental variables	PCA axes			
	1	2	3	4
Ngangao (Nga)	-0.3394	-0.2271	0.2842	0.4218
Chawia (Cha)	-0.5135	-0.2690	-0.5398	-0.2334
Mbololo (Mbol)	0.7462	0.4359	0.1993	-0.1867
pH	0.3754	0.1426	-0.2109	-0.4821
Sand	-0.0028	-0.0254	0.1452	0.0298
Silt	0.0124	0.3947	-0.0802	-0.1862
Clay	-0.2225	-0.3238	-0.1509	0.1459
Na	0.8773	-0.0566	-0.0901	0.1217
Mg	-0.2110	-0.1154	0.5564	0.4496
C	-0.2677	-0.1980	0.4919	0.4850
N	-0.3032	-0.1901	0.5059	0.4808
K	-0.2908	-0.2352	0.4484	0.5640
P	-0.3708	-0.0113	-0.1838	-0.3045

Mg) concentrations (Fig. 6B and Table 3).

The patterns in species composition and their relation to soil variables revealed by RDA were similar to those obtained by PCA, thus confirming the correlations between species and soil variables outlined above. The first RDA axis explained 35% of the species composition and the second axis 12%. Altogether, the soil variables (all canonical axes) explained 70% of the variation in species composition.

Correlation of the species and individual soil properties (Table 4) confirmed that Na and the soil texture were the most important determinants of species distribution; pH, C and nutrients played minor roles. Strong positive correlations with Na were shown by the three species *P. petiti*, *C. zimmermannii* and *S. scheffleri*, but a strong negative correlation with two species (*A. gummifera*, *N. buchananii*). *C. fadenii*, *G. volkensii*, *T. trichocarpa* and *S. scheffleri* all had negative correlations with clay particles. Positive correlations were detected for pH with *S. scheffleri* and *D. integra* and a negative correlation between pH and *P. stuhlmannii*. Ca had a positive correlation with *M. conglomerata* and a negative correlation with *P. petiti*. Two species, *D. integra* and *M. conglomerata*, had significant positive correlations with both N and C. There was a significant positive correlation between P and *A. gummifera* and a negative correlation with *C. zimmermannii* with P. The species *A. adolfi-friedricii*, *C. greenwayi*, *S. guineense* and *T. stapfiana* had no particular correlation with any of the soil variables.

3.4 Seedlings and saplings

The distribution pattern of the mature trees explained

31% of the total variation in the occurrence of seedlings and 51.1% of the saplings. The ordination for seedlings further showed a strong third axis (Eigen value = 0.596), indicating some systematic variations not explained by mature tree species composition. Seedlings were actually found only at Mbololo site where there was a negative (non-significant) correlation between the number of seedlings and the basal area of mature trees.

4 Discussion

The strong relationship between soil extractable Na contents and species composition was unexpected since sodium is not generally considered an essential plant nutrient. More often, high levels of soil Na are considered toxic to plants (Bernstein, 1975). There is some evidence however, that for K deficient soils in particular, Na may substitute for K (Almeida et al., 2010); the ordination of our data carried out to exclude soil Na, in fact, results in K contents being identified as strongly related to axis 1. This would indicate that the effect of K was being masked by Na. The possible substitution of K by Na requires further investigation.

Another unexpected finding is the negative relationship between the abundance of several tree species and clay contents, since higher values of clay generally indicate an improved soil nutrient status (Mengel et al., 2001). Our finding would indicate that the occurrence of tree species in these forests is more related to the negative impact of clay contents on the soil moisture/aeration conditions than to the positive effect of clay on exchangeable nutrient contents.

The positive correlation of *A. gummifera* with P

could be explained by the effect that pH has on the availability of P in the soil. This species was most abundant in Ngangao, the study sites which had the highest soil P ($4.0 \text{ mg}\cdot\text{kg}^{-1}$) and lowest pH (4.1) compared to Chawia and Mbololo. It is known that in the tropics, P is the nutrient which limits the growth of forests (Vitousek, 1984) and that its availability is dependent on pH levels (Brady, 1984). This result shows the distribution of *A. gummifera* to be dependent on P at low pH levels. *C. zimmermannii*, on the other hand, was negatively correlated with P. Furthermore, no correlation was seen with pH, an indication that in this study pH levels enhanced the availability of P and the

extent to which it affected the spatial distribution of some species.

Other species in this study were observed not to have any correlation with any of the soil variables. This is not surprising since studies by Gruszczynska et al. (1991) and Vitousek et al. (1996) showed that soil parameters do not affect spatial differentiation of plant communities; instead other factors such as geodynamic and anthropogenic activities do. In this study therefore, spatial distribution of *A. adolfi-friedricii*, *C. greenwayi* and *S. guineense* were not related to any of the soil variables. However, these are species typically found in tropical mountain forests (FAO, 2000) and in the Taita Hills, where *S. guineense* is endemic (Chege and Bytebier, 2005), their frequencies were relatively higher in Mbololo than in the two other sites; this site is known to be the least disturbed of the three forests. The occurrence of these species in this forest fragment shows their natural distribution and the effect that minimal disturbance has had on this particular fragment.

In so far as the seedlings and saplings are concerned, the significance of the findings is that the seedlings did not respond to the factors to which the mature trees responded. Soil variables did not affect the seedling composition. Therefore other factors were affecting seedling distribution, and these could include factors such as gaps. At Mbololo, there was a trend that the highest numbers of seedlings were found with relatively low basal areas, which may indicate the presence of gaps. The gaps allow sunlight in particular, to reach the forest floor and this stimulates the germination and subsequent growth of seeds that are stored in the soil which would not grow if the conditions are not right. However, as the seedlings continue to grow, other factors emerge and these may include soil variables as shown by the distribution of the saplings.

5 Conclusions

The principal aim of this work was to establish whether there were relationships between spatial distributions of native woody species and some soil variables. Therefore, before planning smaller scale restorations it would be best to establish the levels of soil variables (in particular Na, C and P), pH and soil texture, which were found to be important particularly when targeting specific species composition during restoration. The study showed that, although some of the endemic species were not related at all to any of the soil variables, other species responded to a varying set of variables. Altogether, the soil variables measured explained as much as 70% of the total variation in tree species

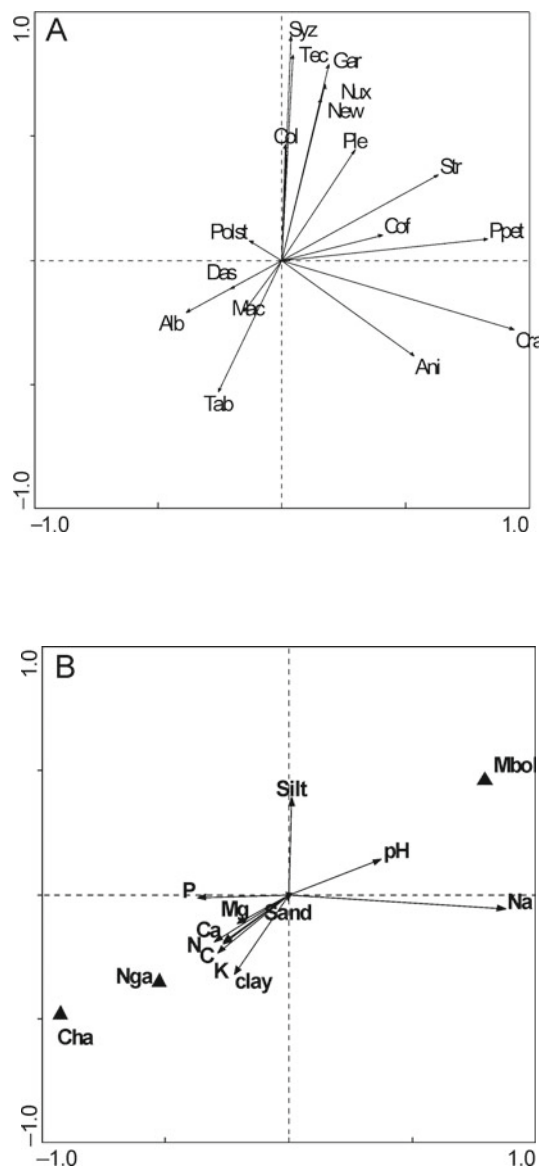


Fig. 6 Ordination diagrams for the species variables (A) and environmental variables (B) for tree stem densities and soil variables in the three study sites. The eigen values for axis 1 and 2 were 0.35 and 0.25, respectively. ▲ denotes the study site.

Table 4 Species correlations with specific soil variables

Species	Clay	Silt	pH	N	C	Ca	K	Na	P
Cra	-0.41	-0.05	0.39	-0.09	-0.05	-0.14	-0.29	0.70	-0.51
Cof	-0.72	0.17	0.31	-0.14	-0.17	-0.17	-0.34	0.25	-0.13
Alb	0.47	-0.34	0.07	-0.32	-0.38	-0.10	-0.10	-0.53	0.49
Das	0.15	-0.26	-0.56	0.52	0.52	0.04	0.56	0.23	-0.19
Gar	-0.56	0.42	0.32	-0.29	-0.23	-0.23	-0.25	0.19	-0.18
Mac	-0.02	-0.11	-0.14	0.58	0.54	0.64	0.51	0.14	-0.47
New	-0.21	0.46	0.07	-0.10	-0.02	0.03	-0.25	0.56	0.05
Polst	-0.09	0.15	-0.48	0.11	0.05	-0.21	0.26	0.02	-0.27
Tec	-0.52	0.51	0.31	-0.51*	-0.35	-0.30	-0.52	0.15	0.23
Str	-0.54	0.17	0.54	-0.19	-0.08	-0.09	-0.43	0.68	-0.11
Ppet	-0.32	0.21	0.23	-0.46	-0.31	-0.50	-0.53	0.68	-0.32

Note: Values in bold denote significant correlations ($p < 0.05$).

composition.

Disturbance may have accounted for the distribution of the species not related to soil properties. High frequency, of endemic species in particular, was associated with areas of low disturbance where their populations remained intact. This would suggest that these species could be generally used in restoration projects. The distributions of both seedlings and saplings were evaluated and showed that seedlings responded most to the presence of gaps while the distributions of saplings depended on factors similar to those to which mature tree species responded. This suggests that without disturbance these species would be indifferent to the variation in soil properties that we have demonstrated for these forest areas. However, disturbance may also offer opportunity to manipulate restoration by facilitating and enhancing succession through planting of the desired species. Seedlings responded most to presence of gaps while the distributions of saplings depended on factors similar to those which mature tree species responded to. This suggests that conditions for regeneration need to be taken into consideration, e.g. by preparing gaps for seedling establishment, where there is need to manipulate species composition.

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References

- Almeida J C R, Laclau J-P, Concalves J L de Moraes, Ranger J, Saint-André L. 2010. A positive growth response to NaCl applications in *Eucalyptus* plantations established on K-deficient soils. *Forest Ecol Manag*, 259: 1786–1795
- Beentje H J. 1988. An ecological and floristical study of the forests of the Taita Hills, Kenya. *Utafiti*, 10: 1, 23–66
- Bernstein L. 1975. Effects of salinity and sodicity on plant growth. *Ann Rev Phytopathol*, 13: 295–313
- Black C C, Evans D D, White J L, Ensminger L E, Clark F E. 1965. *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*. Madison, Wisconsin, USA: American Society of Agronomy, Inc
- Bouyoucos G J. 1962. Hydrometer method improved for making particle size analysis of soils. *Agron J*, 53: 464–465
- Brady N C. 1984. *The nature and properties of soils*. 9th edn. New York, USA: Macmillan Publishers
- Bremner J N. 1965. Total nitrogen. In: Black C C, Evans D D, White J L, Ensminger L E, Clark F E, eds. *Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties*. Madison, Wisconsin, USA: American Society of Agronomy, Inc, 1149–1178
- Bytebier B. 2001. Taita Hills Biodiversity Project Report. National Museums of Kenya Nairobi
- Chege J, Bytebier B. 2005. Vegetation structure of four small fragments in Taita Hills, Kenya. *J East Afr Nat Hist*, 94(1): 231–234

- Conservation International. 2005. Biodiversity hotspots. <http://www.biodiversityhotspots.org/Pages/default.aspx>. Accessed 23 Nov 2008
- Conservatoire et Jardin botanique de la Ville de Genève and South African National Biodiversity Institute. 2009. African Plants Database (Version 3.3). <http://www.ville-ge.ch/musinfo/bd/cjb/africa/resultat.php>. Accessed 18 Jun 2010
- Echeverría C, Newton A C, Lara A, Benayas J M R, Coomes D A. 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecol Biogeogr*, 16(4): 426–439
- Evans J. 1992. *Plantation Forestry in the Tropics*. 2nd edn. New York: Oxford University Press
- FAO. 1990. FAO-UNESCO. Soil Map of the World. Revised Legend. World Resources Report 60. Food and Agriculture Organization of the United Nations-Rome. Rome: FAO
- FAO. 2000. Africa: Ecological Zones. FAO Global Forest Assessment. FAO Forestry Paper
- Fox J F. 1979. Intermediate-disturbance hypothesis. *Science*, 204: 1344–1345
- Grime J P, Thompson K, Hunt R, Hodgson J G, Cornelissen J H C, Rorison I H, Hendry G A F, Ashenden T W, Askew A P, Band S R, Booth R E, Bossard C C, Campbell B D, Cooper J E L, Davison A W, Gupta P L, Hall W, Hand D W, Hannah M A, Hiller S H, Hodgkinson D J, Jalili A, Liu Z, Mackey J M L, Matthews N, Mowfourth M A, Neal A M, Reader R J, Reiling K, Ross-Fraser W, Spencer R E, Sutton F, Tasker D E, Thorpe P C, Whitehouse J. 1997. Integrated screening validates primary axes of specialization in plants. *Oikos*, 79: 259–281
- Gruszczynska B, Wierzchowska U, Wyszomirski T. 1991. Vegetation of the Plock
- Habarurema E, Steiner K G. 1997. Soil suitability classification by farmers in southern Rwanda. *Geoderma*, 75(1–2): 75–87
- Hironka M, Forsberg M A, Neiman J R K E. 1991. The relationship between soils and vegetation. In: Harvey A E, Neuenschwander L F, eds. *Proceedings: Management and Productivity of Western-Montane Forest Soils*. USDA Forest Service, Intermountain Research Station, INT-280, Boise, ID, 29–31
- Hobbs R J, Huenneke L F. 1992. Disturbance diversity and invasion: implications for conservation. *Conserv Biol*, 6: 324–337
- Jaetzold R, Schmidt H. 1983. *Farm Management Handbook of Kenya*. Vol. II East Kenya. Ministry of Agriculture, Kenya
- Jafari M A, Chahouki Z, Tavili A, Azarnivand H. 2003. Soil-vegetation relationships in Hoz-e-Soltan of Qom Province, Iran. *Pakistan J Nutr*, 2(6): 329–334
- John R, Dalling J W, Harms K E, Yavitt J B, Stallard R F, Mirabello M, Hubbell S P, Valencia R, Navarrete H, Vallejo M, Foster R B. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences, USA*, 864–869
- Jongman R H G, ter Braak C J F, van Tongren O F R. 1987. *Data analysis in Community and Landscape Ecology*. Pudoc, Wageningen
- Koerselman W, Meuleman A F M. 1996. The Vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J Appl Ecol*, 33: 1441–1450
- Lepš J, Šmilauer T. 2005. *Multivariate Analysis of Ecological data*. Course material. Faculty of Biological Sciences, University of Bohemia
- Madoffe S, Hertel G D, Rogers P, O'Connell B, Killenga R. 2006. Monitoring of selected Eastern Arc forests in Tanzania. *Afr J Ecol*, 44: 171–177
- Mengel K E A, Kirkby E A, Kosegarten H, Appel T. 2001. *Principles of Plant Nutrition*. 5th edn. Dordrecht, the Netherlands: Kluwer Academic Publishers
- Muhanguzi H D R, Obua J, Oryema-Origa H. 2007. The effect of human disturbance on tree species composition and demographic structure in Kalinzu Forest Reserve, Uganda. *Afr J Ecol*, 45(3): 2–10
- Myers N, Mittermeier R A, Mittermeier C G, da Fonseca G A B, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403 (6772): 853–858
- Okalebo J R, Gathua K W, Woomer P L. 2002. *Laboratory Methods of Soil and Plant Analysis: A Working Manual*. 2nd edn. Nairobi, Kenya: TSBF-CIAT and SACRED Africa
- Omoro L M A, Pellikka P K E, Rogers P C. 2010. Tree species diversity, richness, and similarity between exotic and indigenous forests in the cloud forests of Eastern Arc Mountains, Taita Hills, Kenya. *J Forest Res*, 21(3): 255–264
- Onainidia M, Domingues I, Ibizu I, Garbisu C, Amezaga I. 2004. Vegetation diversity and vertical structure as indicators of forest disturbance. *Forest Ecol Manag*, 195(3): 341–354
- Pellikka P, Lötjönen M, Siljander M, Lens L. 2009. Airborne remote sensing of spatiotemporal change (1955–2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. *Int J Appl Earth Obs*, 11(4): 221–232
- Peter A, Marion B. 2008. Past and present ecology of Laetoli Tanzania. *J Hum Evol*, 54: 78–98
- Rixen C, Haag S, Kulakowski D, Bebi P. 2007. Natural avalanche disturbance shapes plant diversity and species composition in subalpine forest belt. *J Veg Sci*, 18(5): 735–742
- Rogo L, Ogue N. 2000. The Taita Hills Forest Remnants: a disappearing world heritage. *Ambio*, 29: 522–523
- Rogers P C. 1996. *Disturbance ecology and forest management: a review of the literature*. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station, 16
- Rogers P C, O'Connell B, Mwangombe J, Madoffe S, Hertel G. 2008. Forest health monitoring in the Ngangao forest, Taita Hills, Kenya: A five year assessment of change. *J East Afr Nat Hist*, 97(1): 3–17
- Ruggiero P G C, Batalha M A, Pivello V R, Meirelles S T. 2002. Soil-vegetation relationships in cerrado (*Brazilian Savanna*) and semideciduous forest, Southeastern Brazil. *Plant Ecol*, 160: 1–16
- Salminen H. 2004. A geographic overview of Taita Hills, Kenya. In: Pellikka P, Ylhäisi J, Clark B, eds. *Seminar, Reports and Journal of a Field Excursion to Kenya*. Expedition Reports of Department of Geography, University of Helsinki. Helsinki, Finland
- Sanchez P, Palm C. 1996. Forest influences. *Unasylva*, 185
- Schulte A, Ruhayat D. 1998. *Soils of Tropical Forests Ecosystems: Characteristics, Ecology and Management*. Berlin: Springer-Verlag
- SPSS. 2007. SPSS for Windows, Release 16.0.0. Chicago, USA: SPSS
- Swain M D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *J Ecol*, 84(3): 419–428
- The Taita Biodiversity Conservation Project. 2004. Eastern Arc Mountains Information Source. <http://www.easternarc.org>. Accessed 24 Aug 2010
- Ukpong I E. 1995. An ordination study of mangrove swamp communities in West Africa. *Vegetatio*, 116: 147–159
- Ukpong I E, Areola O O. 1995. Relationship between vegetation gradients and soil variables of mangrove swamps in

- south-eastern Nigeria. *Afr J Ecol*, 33: 14–24
- USDA Forest Service. 2007. Forest Inventory and Analysis National Program. <http://www.fia.fs.fed.us/library/field-guides-methods-proc>. Accessed 18 Jun 2010
- van Breemen N, Finzi A C, Canham C D. 1997. Canopy tree-soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. *Can J For Res*, 27: 1110–1116
- van Noordwijk M, Purnomosidhi P. 1995. Root architecture in relation to tree-soil-crop interaction and shoot pruning in agroforestry. *Agrofor Syst*, 30: 161–173
- Vincent R C, Meguro N. 2008. Influence of soil properties on the abundance of plant species in ferruginous rocky soils vegetation, southeastern Brazil. *Rev Bras Bot*, 31(3): 377–388
- Vitousek P M. 1984. Litter fall, nutrient cycling and nutrient limitation in tropical forests. *Ecology*, 65: 285–298
- Vitousek P, Carla D, Loope L, Westbrooks R. 1996. Biological invasions as global environmental change. *Am Sci*, 84(5): 468–478
- Walkley A, Black I A. 1934. An examination of Degtjareff method for determining soil organic matter and proposed modification of the chromic acid titration method. *Soil Sci*, 37: 29–38
- Wilder C, Brooks T, Lens L. 1998. Vegetation structure and composition of the Taita Hills forest. *J East Afr Nat Hist*, 87: 181–187
- Woodward F I, Williams B G. 1987. Climate and plant distribution at global and local scales. *Vegetatio*, 69(1–3): 187–197
- Xu X L, Ma K M, Fu B J, Song C J, Liu W. 2008. Relationships between vegetation and soil and topography in a dry warm river valley, SW China. *Catena*, 75(2): 138–145
- Zhang J T, Ru W M, Li B. 2006. Relationships between vegetation and climate on the Loess Plateau in China. *Folia Geobot*, 41(2): 151–163

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