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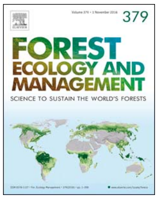

Interactions between native tree species and environmental variables along forest edge-interior gradient in fragmented forest patches of Taita Hills, Kenya

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ABSTRACT

Comparative investigations were undertaken in five forest fragments (Chawia, Fururu, Mbololo, Ngangao and Vuria) of varying sizes in Taita Hills, Kenya to examine the effects of forest edge on soil moisture, nitrogen, phosphorus, potassium, pH, electrical conductivity and organic carbon (hereafter referred to as environmental variables) along forest edge-interior gradient and relate them to tree species distribution and abundance. For each of the forest fragment, belt transects proportional to the forest area were established for data collection. Within each belt transect, plots of 10.0 × 10.0 m were systematically established and replicated three times in a stratum at an interval of between 10.0 and 50.0 m along forest edge-interior gradient depending on the size of the forest fragment for assessment of environmental variables and tree species distribution and abundance. Results showed significant edge effect on the distribution and abundance of dominant and adaptable tree species i.e. *Macaranga conglomerata*, *Albizia gummifera*, *Syzygium guineense*, *Xymalos monospora*, *Tabernaemontana stapfiana* and *Maesa lanceolata* ($p = .012$). Edge effect was also noted among the following environmental variables; soil pH in Mbololo ($p < .001$), Ngangao ($p < .001$) and Vuria ($p = .042$), electrical conductivity ($p = .048$) and nitrogen ($p = .038$) in Fururu and potassium in Mbololo ($p = .002$) and Ngangao ($p = .035$). The distance from the forest edge influenced the distribution and abundance of 36.7% and 36.4% of most abundant species and less abundant species respectively. The environmental variables-tree species relationships established in this study could be utilized in selecting native tree species for rehabilitation programs to restore the degraded sites within the forest fragments.

1. Introduction

Forest fragmentation is among the greatest threats to biodiversity (Pardini et al., 2010; Laurance et al., 2011; Magnago et al., 2014; Magnago et al., 2015), species interactions and ecosystem processes in tropical forests (Steffan-Dewenter et al., 2007; Morris, 2010). Fragmentation of forests into small isolated patches increases susceptibility of forest remnants to edge effects (Matlack, 1993). The microclimate at the forest edge differs from that of the forest interior in attributes such as incident light, humidity, ground and air temperature, wind shear, and wind turbulence that sharply elevate rate of tree mortality and damage and influences most of the biotic variables (Jose et al., 1996; Laurance and Bierregaard, 1997; Laurance et al., 2011). These physical changes affect biological processes such as litter decomposition and nutrient cycling, and the forest structure, composition of vegetation and ecological function along forest edges exposed to non-forested habitats (Bennett and Saunders, 2010).

Effects of increased forest edge alter species interactions by increasing the degree of interaction among edge and forest interior species (Laurance and Bierregaard, 1997; Laurance et al., 2000, 2011). Tree species growing on the edge are usually those adapted to edge microclimates and are often pioneer species found in the early stages of forest succession in any given region (Kupfer and Malanson, 1993). The responses of forest interior species to conditions that develop along the newly created forest edge vary, some species are advantaged and increase in abundance (Bennett and Saunders, 2010) while others are unable to survive in the newly created conditions and hence decline, becoming locally extinct (Laurance, 2002; Bennett and Saunders, 2010).

Edge effects are among the most significant drivers of ecological

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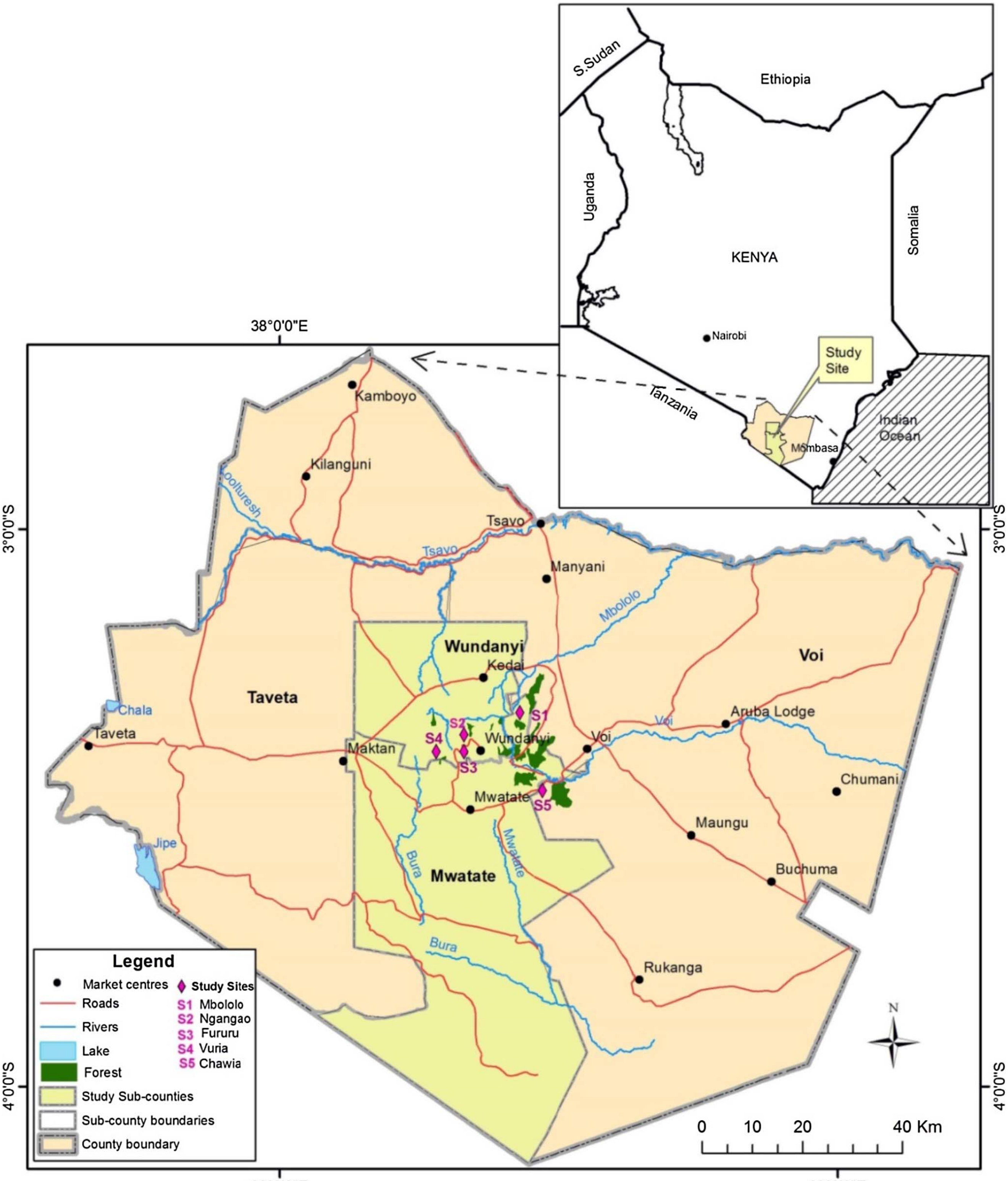

Fig. 1. A map of Taita Taveta County showing the study sites.

change in small forest fragments (Laurance et al., 2011) and are responsible for wide ranging changes in community composition of trees (Laurance et al., 2000, 2006a, 2006b) and lianas (Laurance et al., 2001). Stresses related to edge effects reduce establishment of shade-tolerant species in fragmented forests leading to drastic changes in tree species richness and composition along forest edge-interior gradient (Benítez-Malvido and Martínez-Ramos, 2003; Laurance et al., 2006a, 2006b; Laurance, 2007; Laurance et al., 2011). The distance to which different edge effects penetrate into fragments varies widely, ranging from 10 to 300 m (Jose et al., 1996; Laurance et al., 2002). The environmental conditions progressively change with distance from the forest edge (Matlack, 1993; Jose et al., 1996; Marchand and Houle, 2006; Bergès et al., 2013). Besides, the distribution and occurrence of woody and herbaceous plants in a forest community changes from the forest edge to the interior depending on edge type and aspect (Gehlhausen et al., 2000; Honnay et al., 2002; Marchand and Houle, 2006). Gehlhausen et al. (2000) demonstrated that species abundance was correlated to environmental variables such as canopy openness and soil moisture, two variables that often vary with distance from the forest edge (Cadenasso et al., 1997; Laurance, 2007). Similarly, the differences in species composition from the forest edge to the forest interior have been attributed to the changes in soil nutrients (Aerts et al., 2006; Laurance, 2007).

Spatial variability of soil physical and chemical properties has been reported along forest edge-interior gradient (Redding et al., 2003; Toledo-Aceves and García-Oliva, 2007; Laurance, 2008; Bergès et al., 2013). For example organic carbon, pH, total nitrogen, available phosphorus and soil moisture increases towards forest interior (Camargo and Kapos, 1995; Jose et al., 1996; Aerts and Chapin, 2000; Laurance et al., 2000). Thus, it is has been concluded that the soils on the forest edge have lower nutrient levels than those in forest interior (Toledo-Aceves and García-Oliva, 2007; Laurance, 2007; Laurance, 2008; Bergès et al., 2013). Variation of soil properties along forest edge-interior gradient affects floristic composition in a pattern that is correlated to edaphic variables (Jose et al., 1996; Laurance et al., 2006a, 2006b; Laurance, 2007; Xu, 2008; Zhang et al., 2013). For instance, *Trillium camschatcence* and *Trillium ovatum* are positively correlated to distance to the forest edge and negatively correlated with soil and air temperature, soil variables that vary with distance from forest edge (Jules, 1998; Tomimatsu and Ohara, 2003).

Whereas the results of several soil-vegetation relationships studies have clearly shown that spatial distribution and abundance of species in the forests is related to soil properties (Omoro et al., 2011; Zhang et al., 2013, 2016), the relationships between soil variables and tree species distribution and abundance along forest edge-interior gradient have not been comprehensively explored in fragmented Afromontane forests in tropical regions of Africa including Kenya. Taita Hills forest fragments provide exceptional sites to determine tree species that are best suited to particular sites with respect to the distance from the forest edge, and if this is related to specific soil variables. This is because the prevailing land uses in Taita Hills such as small-scale crop farming, mining and creation of new settlements have produced landscapes dominated by small (< 300 ha) and irregularly shaped forest fragments (Pellikka et al., 2009; Omoro et al., 2010, 2011; Wekesa et al., 2016). Such small and isolated forest fragments are highly vulnerable to the edge effects and deleterious consequences of forest fragmentation (Laurance et al., 2002; Barlow et al., 2006; Cochrane and Laurance, 2008), hence the choice of these sites for this study.

Although several studies on the dynamics of woody plant communities have been undertaken in fragmented forests of Taita Hills (Beentje, 1988; Pellikka et al., 2009; Omoro et al., 2010, 2011; Aerts et al., 2011), only a single study has ever focused on the relationships between tree species and soil properties (Omoro et al., 2011). However, Omoro et al. (2011) did not evaluate the 'edge effects' on soil physical and chemical properties along the gradient from the forest edge to the forest interior and how they are related to spatial distribution and abundance of tree species.

Knowledge about relationships between distribution and abundance of tree species and soil properties is crucial for planning successful forest landscape restoration programs. Therefore, the objective of this study was to determine how the forest edge affects soil physical and chemical properties along a gradient from the forest edge to the forest interior, and the implications on tree species distribution and abundance in fragmented forests of Taita Hills. The following hypotheses were tested: (i) soil physical and chemical properties are different on the forest edge, intermediate forest and forest interior, (ii) the distribution and abundance of tree species reflects the changes in soil physical and chemical properties along forest edge-interior gradient.

2. Materials and methods

2.1. Description of the study area

The study was undertaken in five forest fragments (Mbololo, Ngangao, Chawia, Fururu and Vuria) in Taita Hills (Fig. 1). The approximate areas of the forest fragments studied are as follows; Mbololo (200.0 ha), Ngangao (120.0 ha), Chawia (86.0 ha), Fururu (5.0 ha) and Vuria (1.0 ha) (Beentje, 1988; Pellikka et al., 2009). The forest fragments have similar physical environment, are less than 21 km apart, were once one continuous block, and hence had similar plant communities (Bytebier, 2001; Adriaensen et al., 2006). The long rainy season occurs from March to May and a shorter rainy season in November-December, but the mist and cloud precipitation is a year-round phenomenon in the Hills. The average yearly rainfall is 2000 mm (Pellikka et al., 2009; Republic of Kenya, 2009). The average temperature is 23 °C with variations between 18 °C and 24.6 °C (Republic of Kenya, 2013). The Hills experience lower temperatures of 18.2 °C compared to the lower zones which have an average temperature of 24.6 °C (Republic of Kenya, 2013). The average relative humidity is 79 and 83% for the lower zones and the Hills respectively (Republic of Kenya, 2013).

The soils are predominantly Cambisols originating from weathered gneiss and are often gravely to sandy-loamy and shallow (Sombroek et al., 1982). The soils are well drained and moderately fertile. Majority of Cambisols are in a transitional stage of development from a young soil to a mature one (Sombroek et al., 1982). On the steep slopes and transitional zones, the dominant soil types are regosols, which are shallow soils, have high permeability and low water holding capacity (Sombroek et al., 1982). Due to the favourable climatic and edaphic conditions, the forested land in Taita Hills has been cleared for agriculture and remaining forests have been used for firewood collection, charcoal production and grazing (Pellikka et al., 2009).

2.2. Sampling design

Belt transects and 10.0 × 10.0 m plots were used for data collection along forest edge-interior. Forest edge was defined as the interface between forested ecosystems and farmlands. The size and number of belt transects varied among the forest fragments depending on the fragment size (Table 1). The number of plots also varied among the fragments depending on the size of the forest fragment. Mbololo had a total of 27 plots, Ngangao (15), Chawia (12), Fururu (9) and Vuria (9). Mbololo had 9 plots each on the forest edge, intermediate forest and forest interior, Ngangao (5), Chawia (4), Fururu (3) and Vuria (3). Transects were laid up slope from the edge of the forest to the forest interior.

2.2.1. Tree data collection

The assessment of tree species was undertaken in plots and sub-plots established within the belt transects. Within each belt transect, plots of 10.0 × 10.0 m were systematically established and replicated three times in a stratum at an interval of between 10.0 and 50.0 m along the

Table 1
Sampling frame and intensity for the study. The size and the number of transects are proportional to the fragment size.

Forest fragment	Area (ha)	Transect dimensions (m)		Number of transects	Number of plots
		Length	Width		
Mbololo	200.0	150.0	40.0	9	27
Ngangao	120.0	120.0	40.0	5	15
Chawia	86.0	90.0	40.0	4	12
Fururu	5.0	60.0	40.0	3	9
Vuria	1.0	30.0	40.0	3	9

forest edge-interior gradient depending on the size of the forest fragment. All the trees with diameter at breast height (DBH) greater than 2.5 m in the 10.0 × 10.0 m plot were identified by their botanical names and recorded.

Data on the distribution and abundance of *Macaranga conglomerata*, *Albizia gummifera*, *Syzygium guineense*, *Xymalos monospora*, *Tabernaemontana stapfiana* and *Maesa lanceolata*, the six dominant and adaptable tree species (Omoro et al., 2010; Aerts et al., 2011) was also collected in all the plots. These species are indicator species sensitive to environmental changes and quickly respond to adverse ecosystem changes; hence the species are used as a diagnostic proxy for natural forest ecosystems health (Aerts et al., 2011; Wekesa et al., 2016).

2.2.2. Soil sampling

Three replicate of soil samples were randomly collected using soil auger at depths of 0–15 cm and 15–30 cm (Ojoyi et al., 2014). The soil samples were composited to obtain a representative sample for the plot, packaged in zip lock bags and taken to the laboratory for analyses to determine the levels of moisture, nitrogen, phosphorus, potassium, pH, electrical conductivity (EC) and organic carbon. In total, 432 soil samples were collected from 72 plots spread across five forest fragments.

2.3. Soil analysis for physical and chemical properties

Prior to the analysis, the soil samples were air-dried and sieved using 2.0 mm sieve. Phosphorus and nitrogen were determined using Olsen and Kjeldahl methods respectively (Okalebo et al., 2002). Measurements of potassium involved extraction of soil samples using ammonia acetate pH 7 followed by spraying the contents into the flame photometer model Corning M 410 for potassium measurement (Okalebo et al., 2002). Organic carbon was determined using Walkley-Black method through complete oxidation (Walkley and Black, 1934). Determination of soil pH and electrical conductivity (EC) involved the use of soil pH meter and electrical conductivity meter respectively as prescribed by Anderson and Ingram (1993) and Okalebo et al. (2002). Soil moisture content was determined using oven-dry method (Okalebo et al., 2002).

2.4. Data analysis

One-way Analysis of Variance (ANOVA) and Tukey's post hoc test were used to test the presence or absence of significant effects in edaphic factors (moisture content, nitrogen, phosphorus, potassium, pH, EC and organic carbon) within and among the forest fragments along forest edge-interior gradient (forest edge, intermediate forest and forest interior) at 5% probability significance threshold.

Canonical Correspondence Analysis (CCA) was used to determine the relationships between tree species and edaphic factors as well as species association along the forest edge-interior gradient. To avoid rare tree species distorting the results, only tree species that occurred in at least 6% of the plots were included in the analysis. Tree species classification involved two categories: most abundant and less abundant. Most abundant tree species were those species that occurred in at least 11% of the sampled plots while less abundant tree species were those that occurred in at least 6% but less than 11% of the sampled plots. Prior to undertaking CCA, the length of the gradient, which is an estimate of species heterogeneity, was determined using Detrended Correspondence Analysis (DCA). When the length of the gradient from DCA is less than three standard deviations (SD), linear models such as Principal Component Analysis (PCA) and Redundancy Analysis (RDA) are appropriate. When the length of the gradient is greater than four SD, unimodal methods i.e. Correspondence Analysis (CA), Canonical Correspondence Analysis (CCA) and Detrended Correspondence Analysis (DCA) are appropriate (Ter Braak and Smilauer, 2002). When the length of the gradient lies between three and four SD, either of the ordination methods that explain better can be used (Leps and Smilauer, 2003). Besides, the constrained or unconstrained nature of the ordination determines the ordination technique to be used (Ter Braak and Smilauer, 2002).

Exploration of the response of tree species to edaphic factors and distance from the forest edge involved application of DCA taking into account all the species that occurred in the sampled plots in all the five forest fragments. Preliminary DCA test revealed that the distribution and abundance of tree species exhibited unimodal responses to the edaphic factors and distance from the forest edge with gradient length of five standard deviations (SD). Since the gradient length was greater than four SD, CCA was found the most appropriate method for analysis (Ter Braak and Smilauer, 2002). The effect of edaphic factors and distance from the forest edge on the distribution and association of six dominant and adaptable tree species, most abundant and less abundant tree species involved the application of CCA with automatic forward selection using 1000 permutations. The determination of the influence of six dominant and adaptable tree species on the distribution of rare/less-abundant tree species also used CCA. Significance testing at the 95% probability level made use of Monte-Carlo Permutation Test (MCPT).

3. Results

3.1. Variation of environmental variables along forest edge-interior gradient

The soil moisture content (%) varied significantly along the forest edge-interior gradient in Chawia ($F_{(1,\ 2)} = 47.47$; $p < .001$), Fururu ($F_{(1,\ 2)} = 12.96$; $p < .001$), Ngangao ($F_{(1,\ 2)} = 9.97$; $p < .001$) and Vuria ($F_{(1,\ 2)} = 11.25$; $p < .001$) (Table 2). However, no significant variations in soil moisture content were observed in Mbololo ($F_{(1,\ 2)} = 1.45$; $p = .235$). Chawia had significantly higher soil moisture content in the forest interior while in Fururu and Ngangao, the intermediate forest exhibited significantly higher soil moisture content than the forest edge and interior. Soil moisture content in Vuria was higher at the edge of the forest than in the intermediate forest and forest interior.

The results showed no significant variation in soil pH along the forest edge-interior gradient in Chawia ($F_{(1,\ 2)} = 0.36$; $p = .700$) and Fururu ($F_{(1,\ 2)} = 0.41$; $p = .667$). However, Mbololo ($F_{(1,\ 2)} = 15.48$; $p = .001$) and Ngangao ($F_{(1,\ 2)} = 13.21$; $p = .001$) had significantly higher soil pH at the edge of the forest than in the intermediate forest and the forest interior. Vuria had significantly lower soil pH at the edge of the forest than in the intermediate forest and the forest interior ($F_{(1,\ 2)} = 3.63$; $p = .042$). The EC was not significantly different along the forest edge-interior gradient in Chawia ($F_{(1,\ 2)} = 0.11$; $p = .896$), Mbololo ($F_{(1,\ 2)} = 1.01$; $p = .367$), Ngangao ($F_{(1,\ 2)} = 0.60$; $p = .555$) and Vuria ($F_{(1,\ 2)} = 0.15$; $p = .861$). Fururu had significantly higher EC at the edge of the forest than the forest interior and intermediate forest ($F_{(1,\ 2)} = 3.44$; $p = .048$) (Table 3).

In Chawia, there were no significant variations in organic carbon

Table 2

Comparison of mean soil moisture (percentage) along the forest edge-interior gradient for the five forest fragments in Taita Hills. The presented values are means with standard error of mean. Values with similar letters in superscripts in the same row are not significantly different at $p \leq .05$ level.

Forest fragment	Forest edge-interior gradient				
	Forest edge	Intermediate forest	Forest interior	*p* value	LSD
Chawia	1.50 ± 0.00^a	1.65 ± 0.04^a	2.23 ± 0.08^b	< .001	0.171
Fururu	2.77 ± 0.15^b	3.51 ± 0.53^b	1.75 ± 0.11^a	< .001	0.692
Mbololo	1.53 ± 0.05^a	1.64 ± 0.07^a	1.65 ± 0.04^a	.235	0.154
Ngangao	1.25 ± 0.02^a	1.35 ± 0.02^b	1.24 ± 0.02^a	< .001	0.057
Vuria	3.82 ± 0.44^b	2.56 ± 0.12^a	2.48 ± 0.12^a	< .001	0.555

Table 3

Comparison of mean soil pH and electrical conductivity along the forest edge-interior gradient for the five forest fragments in Taita Hills. The presented values are means with standard error of mean. Values with similar letters in superscripts in the same row are not significantly different at $p \leq .05$ level.

Forest fragment	Soil property	Forest edge-interior gradient				
		Forest edge	Intermediate forest	Forest interior	*p* value	LSD
Chawia	pH	5.58 ± 0.26^{a}	5.34 ± 0.14^{a}	5.62 ± 0.32^{a}	.700	0.720
	EC (mS/cm)	0.107 ± 0.019^{a}	0.123 ± 0.019^{a}	0.116 ± 0.032^{a}	.896	0.070
Fururu	pH	6.02 ± 0.19^{a}	6.01 ± 0.13^{a}	5.85 ± 0.10^{a}	.667	0.430
	EC (mS/cm)	0.132 ± 0.021^{b}	0.080 ± 0.010^{a}	0.093 ± 0.011^{ab}	.048	0.043
Mbololo	pH	6.10 ± 0.19^{b}	5.25 ± 0.17^{a}	4.79 ± 0.14^{a}	< .001	0.475
	EC (mS/cm)	0.138 ± 0.022^{a}	0.174 ± 0.028^{a}	0.183 ± 0.021^{a}	.367	0.067
Ngangao	pH	5.23 ± 0.102^{b}	4.69 ± 0.069^{a}	4.72 ± 0.077^{a}	< .001	0.239
	EC (mS/cm)	0.155 ± 0.037^{a}	0.123 ± 0.017^{a}	0.121 ± 0.013^{a}	.555	0.07
Vuria	pH	5.26 ± 0.09^{a}	5.64 ± 0.105^{b}	5.67 ± 0.153^{b}	.042	0.351
	EC (mS/cm)	0.074 ± 0.008^{a}	0.069 ± 0.011^{a}	0.076 ± 0.009^{a}	.861	0.028

Table 4

Comparison of mean organic carbon, nitrogen, phosphorus and potassium along the forest edge-interior gradient for the five forest fragments in Taita Hills. The presented values are means with standard error of mean. Values with similar letters in superscripts in the same row are not significantly different at $p \leq .05$ level. OC = Organic Carbon (%); N = Nitrogen (%); P = Phosphorus (ppm) and K = Potassium (ppm).

Forest fragment	Soil property	Forest edge	Intermediate forest	Forest interior	*p* value	LSD
Chawia	OC (%)	6.98 ± 0.86^{a}	6.94 ± 0.98^{a}	9.52 ± 2.06^{a}	0.345	4.05
	N (%)	0.59 ± 0.17^{a}	0.63 ± 0.15^{a}	0.72 ± 0.18^{a}	0.855	0.48
	P (ppm)	5.0 ± 0.58^{a}	7.0 ± 1.26^{a}	11.0 ± 4.62^{a}	0.265	8.0
	K (ppm)	120.87 ± 15.39^{a}	89.74 ± 9.16^{a}	88.14 ± 9.85^{a}	0.102	33.96
Fururu	OC (%)	4.94 ± 0.78^{a}	4.17 ± 0.65^{a}	4.74 ± 0.62^{a}	0.703	2.025
	N (%)	0.79 ± 0.04^{b}	0.64 ± 0.05^{ab}	0.57 ± 0.08^{a}	0.038	0.17
	P (ppm)	5.0 ± 1.02^{a}	5.0 ± 0.64^{a}	5.0 ± 0.40^{a}	0.997	2.20
	K (ppm)	111.96 ± 21.12^{a}	77.81 ± 13.06^{a}	83.79 ± 11.0^{a}	0.278	46.45
Mbololo	OC (%)	9.14 ± 0.92^{a}	10.08 ± 1.01^{a}	11.56 ± 0.87^{a}	0.192	2.641
	N (%)	0.81 ± 0.078^{a}	0.81 ± 0.08^{a}	0.93 ± 0.08^{a}	0.458	0.23
	P (ppm)	14.0 ± 1.84^{a}	12.0 ± 1.63^{a}	15.0 ± 1.75^{a}	0.430	4.9
	K (ppm)	222.20 ± 31.92^{b}	143.10 ± 15.77^{a}	112.60 ± 13.82^{a}	0.002	62.09
Ngangao	OC (%)	6.91 ± 0.68^{a}	7.09 ± 0.80^{a}	8.59 ± 1.05^{a}	0.321	2.44
	N (%)	0.60 ± 0.07^{a}	0.53 ± 0.06^{a}	0.67 ± 0.06^{a}	0.358	0.19
	P (ppm)	8.0 ± 1.32^{a}	12.0 ± 2.79^{a}	11.0 ± 1.44^{a}	0.404	5.60
	K (ppm)	96.48 ± 15.94^{b}	54.16 ± 6.04^{a}	72.35 ± 8.96^{ab}	0.035	31.74
Vuria	OC (%)	5.591 ± 0.44^{a}	4.84 ± 0.60^{a}	5.12 ± 0.44^{a}	0.576	1.47
	N (%)	0.58 ± 0.06^{a}	0.57 ± 0.06^{a}	0.45 ± 0.04^{a}	0.156	0.16
	P (ppm)	18.0 ± 4.26^{a}	23.0 ± 4.81^{a}	23.0 ± 5.24^{a}	0.690	14.0
	K (ppm)	163.10 ± 36.51^{a}	246.50 ± 38.83^{a}	221.50 ± 21.26^{a}	0.209	96.69

($F_{(1,\ 2)} = 1.10$; $p = .345$), nitrogen ($F_{(1,\ 2)} = 0.16$; $p = .855$), phosphorus ($F_{(1,\ 2)} = 1.38$; $p = .265$) and potassium ($F_{(1,\ 2)} = 2.44$; $p = .102$) along the forest edge-interior gradient (Table 4). Similarly, no significant variations in organic carbon ($F_{(1,\ 2)} = 0.56$; $p = .576$), nitrogen ($F_{(1,\ 2)} = 2.01$; $p = .156$), phosphorus ($F_{(1,\ 2)} = 0.38$; $p = .690$) and potassium ($F_{(1,\ 2)} = 1.67$; $p = .209$) were observed in Vuria along the gradient from the edge of the forest to the forest interior. In Fururu, soil nitrogen was significantly higher at the forest edge than in the intermediate forest and the forest interior ($F_{(1,\ 2)} = 3.77$; $p = .038$). However, organic carbon ($F_{(1,\ 2)} = 0.36$; $p = .703$), phosphorus ($F_{(1,\ 2)} = 0.00$; $p = .997$) and potassium ($F_{(1,\ 2)} = 1.35$; $p = .278$) were not significantly different along the forest edge-interior gradient (Table 4). Potassium varied significantly along the forest edge-interior gradient in Mbololo ($F_{(1,\ 2)} = 6.58$; $p = .002$) while organic carbon ($F_{(1,\ 2)} = 1.68$; $p = .192$), nitrogen ($F_{(1,\ 2)} = 0.79$; $p = .458$) and phosphorus ($F_{(1,\ 2)} = 0.85$; $p = .430$) were not significantly affected by the edge effect. Similar to Mbololo, organic carbon ($F_{(1,\ 2)} = 1.17$; $p = .321$), nitrogen ($F_{(1,\ 2)} = 1.05$; $p = .358$) and phosphorus ($F_{(1,\ 2)} = 0.93$; $p = .404$) showed no significant differences along the forest edge-interior gradient in Ngangao. However, potassium was significantly higher at the edge of the forest than in the intermediate forest and forest interior ($F_{(1,\ 2)} = 3.64$; $p = .035$) (Table 4).

3.2. Interaction between dominant and adaptable tree species and environmental variables

Canonical Correspondence Analysis (CCA) model for the relationship between the six dominant and adaptable species (*Macaranga conglomerata*, *Albizia gummifera*, *Syzygium guineense*, *Xymalos monospora*, *Tabernaemontana stapfiana* and *Maesa lanceolata*) and environmental variables (MCPT; 1000 Permutations) was significant for distance from the forest edge ($F_{(1000)} = 2.76$; $p = .012$), EC ($F_{(1000)} = 2.53$; $p = .028$), potassium ($F_{(1000)} = 2.39$; $p = .031$) and soil moisture ($F_{(1000)} = 2.46$; $p = .037$). However, soil pH ($F_{(1000)} = 2.15$; $p = .068$), nitrogen ($F_{(1000)} = 0.41$; $p = .838$), phosphorus ($F_{(1000)} = 1.50$; $p = .187$) and organic carbon ($F_{(1000)} = 0.22$; $p = .947$) were not significant in the model.

Albizia gummifera had large abundance within the forests' areas whose soils were saline and had high organic carbon content (Fig. 2). However, there was a negative correlation for *A. gummifera* with soil moisture. Phosphorus and nitrogen had a large positive correlation with *M. conglomerata*. *Xymalos monospora* was more abundant in areas within the forests that had high concentration of potassium in soil. Moreover, soil moisture had a positive relationship with *X. monospora*. *Tabernaemontana stapfiana* had large positive correlation with soil pH and

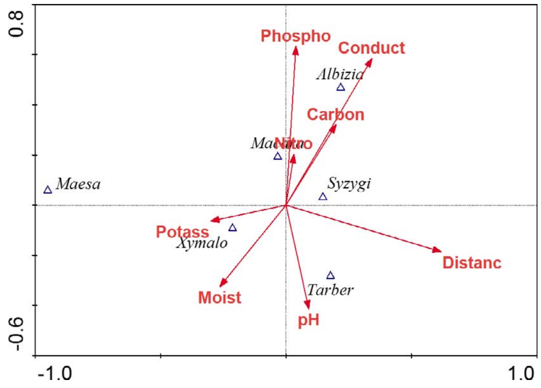

Fig. 2. Canonical Correspondence Analysis (CCA) triplot of six adaptable and dominant tree species and environmental variables in five forest fragments, Taita Hills. Potass = Potassium, Moist = Soil moisture, Conduct = Electrical conductivity, Distanc = Distance from forest edge, Phospho = Phosphorus, Nitro = Nitrogen.

distance from the forest edge. *Syzygium guineense* had a positive relationship with organic carbon and EC. However, the abundance of *M. lanceolata* exhibited no correlation with the environmental variables.

3.3. Interaction between most abundant tree species and environmental variables

The CCA model was significant for EC ($F_{(1000)} = 3.48$; $p = .001$), distance from forest edge ($F_{(1000)} = 2.89$; $p = .001$) and soil pH ($F_{(1000)} = 1.77$; $p = .020$). However, the CCA model was not significant for potassium ($F_{(1000)} = 1.60$; $p = .064$), phosphorus ($F_{(1000)} = 0.98$; $p = .461$), moisture ($F_{(1000)} = 1.48$; $p = .087$), organic carbon ($F_{(1000)} = 1.47$; $p = .081$) and nitrogen ($F_{(1000)} = 1.56$; $p = .052$). The distance from the forest edge had a highly positive correlation with species such as *Tabernaemontana stapfiana*, *Psychotria petitii*, *Chassalia discolor*, *Newtonia buchananii*, *Oxyanthus speciosus*, *Pauridiantha paucinervis* and *Strombosia scheffleri* among other species (Fig. 3). There was a strong positive correlation between potassium and *Xymalos monospora*, *Lepidotrichilia volkensii*, *Cussonia spicata* and *Neoboutonia macrocalyx*. *Dasylepis integra*, *Brucea antidysenterica*, *Garcinia volkensii*, *Phoenix reclinata* and *Pleiocarpa pycnantha* had a high positive correlation with soil pH. Phosphorus had a large positive correlation with *Turraea holstii* and *Millettia oblata*. The EC and nitrogen had a strong positive relationship with *Albizia gummifera* and *Cola greenwayi* whereas *Crabia zimmermannii* exhibited slightly positive correlation with organic carbon. There was no relationship between *Rytigynia uhligii* and *Maytenus senegalensis* with any of the environmental variables studied.

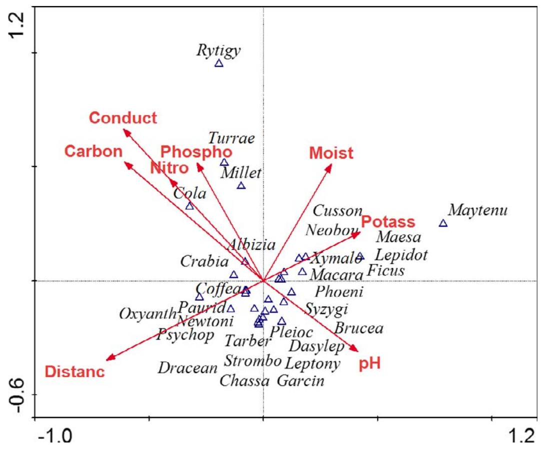

Fig. 3. Canonical Correspondence Analysis (CCA) of most abundant tree species and environmental variables for the five forest fragments in Taita Hills. Potass = Potassium, Moist = Soil moisture, Conduct = Electrical conductivity, Distanc = Distance from forest edge, Phospho = Phosphorus, Nitro = Nitrogen.

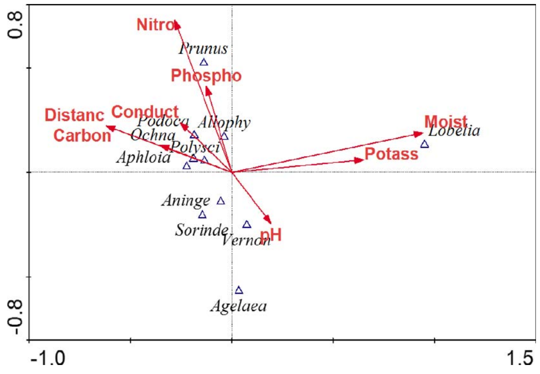

Fig. 4. Canonical Correspondence Analysis (CCA) of less abundant tree species and environmental variables in the five forest fragments of Taita Hills. Potass = Potassium, Moist = Soil moisture, Conduct = Electrical conductivity, Distanc = Distance from forest edge, Phospho = Phosphorus, Nitro = Nitrogen.

3.4. Interaction between less abundant tree species and environmental variables

The CCA model was significant for soil moisture ($F_{(1000)} = 3.30$; $p = .044$), nitrogen ($F_{(1000)} = 2.02$; $p = .017$) and distance from the forest edge ($F_{(1000)} = 1.96$; $p = .021$). However, the model was not significant for organic carbon ($F_{(1000)} = 1.37$; $p = .202$), EC ($F_{(1000)} = 0.79$; $p = .658$), soil pH ($F_{(1000)} = 0.70$; $p = .754$), potassium ($F_{(1000)} = 0.66$; $p = .752$) and phosphorus ($F_{(1000)} = 0.43$; $p = .934$). Less abundant species such as *Prunus africana* and *Allophylus abyssinicus* showed a highly positive correlation with nitrogen and phosphorus (Fig. 4). *Podocarpus latifolius*, *Ochna holstii*, *Aphloia theiformis* and *Polyscias fulva* had positive correlation with organic carbon, EC and distance from the forest edge. *Lobelia giberroa* had a high positive correlation with soil moisture and potassium. *Vernonia auriculifera* and *Agelaea pentagyna* had a strong positive correlation with soil pH. Similarly, *Aningeria robusta* and *Sorindeia madagascariensis* were correlated with soil pH.

4. Discussion

4.1. Effects of forest edge on environmental variables

The results support our hypothesis that soil physical and chemical properties were dependent on the distance from the forest edge. The distance from the forest edge strongly influenced soil moisture along forest edge-interior gradient. In Chawia, Fururu, Ngangao and Mbololo, soil moisture was higher in the intermediate forest and forest interior than on the forest edges. Many studies (Camargo and Kapos 1995; Laurance et al., 1998, 2000; Baimas-George, 2012) have shown that soil moisture is higher in the forest interior than on edge. Contrary to most studies, soil moisture in Vuria decreased towards the forest interior most likely because of very steep gradient that increased sharply towards the forest interior affecting soil moisture adversely as previously demonstrated by Huat et al. (2006).

The soil pH also varied with distance from the forest edge. In Fururu, Mbololo and Ngangao, the soil pH was moderately acidic at the forest edge but strongly acidic in the forest interior. This is in agreement with findings of previous studies which have shown that soil pH declines from forest edge to the interior (Aerts et al., 2006; Wuyts et al., 2013). The soil pH was moderately acidic on the forest edge, intermediate forest and forest interior in Chawia and Vuria. Chawia and Vuria are heavily disturbed (Pellikka et al., 2009; Wekesa et al., 2016), and therefore, the ecological conditions on the forest edges and in the intermediate forest and forest interior does not differ much; this could explain the similarity in soil pH along forest edge-interior gradient. The EC was not affected by the distance from the forest edge in Chawia, Mbololo, Ngangao and Vuria. However, the EC was higher on the forest edge than in the forest interior and intermediate forest in Fururu. Unlike Chawia, Mbololo, Ngangao and Vuria which are surrounded by roads and fallow lands, Fururu is surrounded by intensively cultivated farms. There is heavy use of inorganic fertilizers in the cultivated farms surrounding Fururu and that is why the EC was higher at the edge of the forest than in the forest interior. The EC is dependent on the cation exchange capacity and salinity level in the soil and therefore, application of inorganic fertilizers increases the EC and pH of the soil (Grisso et al., 2009).

Nitrogen content in the soil was affected by the distance from the forest edge and hence varied along forest edge-interior gradient. In Chawia and Mbololo, nitrogen increased towards the forest interior while in Fururu and Vuria, it decreased towards the forest interior. In Ngangao, nitrogen was higher in the forest interior and lower in the intermediate forest. The scenario in Chawia, Mbololo and Ngangao where nitrogen content was higher in the forest interior than on the forest edge is congruent with finding of previous studies (Jose et al., 1996; Aerts and Chapin, 2000; Laurance et al., 2000; Toledo-Aceves and García-Oliva, 2007). In contrast, the decrease in nitrogen content towards the forest interior in Fururu and Vuria was because of two reasons. Firstly, the soils become shallower towards the interior due to the presence of numerous rocks in the interior of Fururu and Vuria as the elevation increases. The shallow soils encumber rapid mineralization of organic matter leading to low nitrogen in the forest interior. Secondly, Fururu is surrounded by intensively cultivated farmlands. The farmlands are regularly cultivated for food crops using inorganic fertilizers. The forest edges that border these inorganically fertilized agricultural farmlands receive nitrogen from fertilizer inputs (Pocewicz and Penelope, 2007) increasing the nitrogen level on the forest edge.

The level of organic carbon in the soil was dependent on the distance from the forest edge. In Mbololo and Ngangao, organic carbon increased towards forest interior. Other related studies have shown that forest edge soils have significantly lower percentage carbon than forest interior soils (Redding et al., 2003; Toledo-Aceves and García-Oliva, 2007; Bergès et al., 2013). On the other hand, organic carbon was higher on the forest edges in Chawia, Fururu and Vuria than in the intermediate forest and forest interior. This diverges from earlier reports that showed forest edge soils have lower organic carbon than the forest interior (Redding et al., 2003; Toledo-Aceves and García-Oliva, 2007; Bergès et al., 2013). Seemingly, the size of the forest fragment influenced the organic carbon dynamics along the forest edge-interior gradient. The small fragments of Chawia, Fururu and Vuria had similar trends for organic carbon levels in the soil along the forest edge-interior gradient, a phenomenon that was also manifested in large forest fragments of Mbololo and Ngangao.

The distance from the forest edge influenced the concentration of phosphorus in the soil. The level of phosphorus was higher in the forest interior than on the forest edges in Chawia, Mbololo, Ngangao and Vuria signifying that the rocks in these forest fragments were of different types along the forest edge-interior gradient. The present results are in agreement with findings by several authors who have indicated that available phosphorus increases towards forest interior (Jose et al., 1996; Laurance et al., 2000; Baimas-George, 2012). However, phosphorus level in Fururu was the same at the forest edge, intermediate forest and forest interior clearly indicating that the rocks occurring in this particular forest were of the same type along the forest edge-interior gradient (Cerozi and Fitzsimmons, 2016). Phosphorus levels in Chawia, Fururu, Mbololo and Ngangao were deficient for plant growth (< 20 ppm). However, in Vuria, the level of phosphorus was sufficient for plant growth (> 20 ppm). According to Okalebo et al. (2002), sufficient levels of phosphorus in the soils range between 20 and 30 ppm. The variation in phosphorus along forest edge-interior gradient could be attributed to the differences in soil pH (Omoro et al., 2011; Cerozi and Fitzsimmons, 2016). Soil pH varies with distance from the forest (Marchand and Houle, 2006) and strongly influences the available phosphorus in tropical forests' soils (Brady, 1984). The difference in the types of rocks was responsible for the variation of phosphorus among the forest fragments as reported by Cross and Schlesinger (1995).

Potassium level in the soil differed between forest edge and the forest interior. In Chawia, Fururu, Mbololo and Ngangao, potassium in the soil was high on the forest edge than in the intermediate forest and forest interior. Prior studies by Bunyan et al. (2012) revealed that available potassium in the soil increases with increasing distance from the forest edge. The results of this study disagree with findings by Bunyan et al. (2012). The present result showing that the level of potassium increased towards forest interior in Vuria agrees with previous findings by Bunyan et al. (2012). Potassium was adequate on the forest edge but deficient in the intermediate forest and the forest interior in Chawia. The situation was different in Fururu and Ngangao where potassium was deficient at the forest edge, in the intermediate forest and the forest interior. In Mbololo, potassium was adequate on the forest edge and in the intermediate forest but deficient in the forest interior while in Vuria, it was adequate at the forest edge, in the intermediate forest and forest interior. The variation in potassium along forest edge-interior gradient and among the forest fragments was attributed to the variation in soil pH and moisture. Soil pH and moisture influence the level of potassium in the soil (Ranade-Malvi, 2011; Maeda, 2012).

A key result of this study was the observation that among the five forest fragments studied, only Vuria had sufficient levels of phosphorus (≥ 20 ppm) and potassium (≥ 117.3 ppm) on the forest edge, in the intermediate forest and forest interior. This means phosphorus and potassium were the nutrients that limited the growth of trees and other plants in the other four forest fragments (Chawia, Fururu, Mbololo and Ngangao). The results reinforces the findings of Vitousek (1984), Wright et al. (2011) and Omoro et al. (2011) which reported that phosphorus and potassium are most critical soil nutrients limiting growth of trees and other plants in tropical forests.

4.2. Interaction between dominant and adaptable tree species and environmental variables

The distribution and abundance of *M. conglomerata*, *A. gummifera*, *S. guineense*, *X. monospora*, *T. stapfiana* and *M. lanceolata* sturdily depended on the distance from the forest edge, EC, potassium and soil moisture levels in the soil. This confirms the hypotheses that the distance from the forest edge and soil properties affect the distribution and abundance of tree species along forest edge-interior gradient. Other related studies (Jules, 1998; Tomimatsu and Ohara, 2003) have shown that tree species in natural forests are positively correlated to distance to the edge. Moreover, studies by Cadenasso et al. (1997), Gehlhausen et al. (2000), Laurance (2007) and Aerts et al. (2011) have shown that tree species abundance is correlated to environmental variables such as soil moisture and potassium, variables that often vary with distance from the forest edge (Cadenasso et al., 1997; Laurance, 2007; Aerts et al., 2011). Nadeau and Sullivan (2015) have also reported that tree species richness in tropical forests is inversely related to the concentration of potassium, calcium and cation exchange capacity.

EC is a measure of soil salinity and therefore, positive or negative changes in soil salinity can affect the distribution and abundance of woody species in tropical forests (Zefferman et al., 2015). Thus, soil salinity affected growth and, distribution and abundance of the six species through ion toxicity, effects on osmotic potential and interference with plant nutrition (Zefferman et al., 2015).

The present results also indicate that soil pH, nitrogen, phosphorus and organic carbon did not influence the distribution and abundance of *M. conglomerata*, *A. gummifera*, *S. guineense*, *X. monospora*, *T. stapfiana* and *M. lanceolata*. This was expected because in tropical forests, nitrogen and organic carbon are sufficiently available for absorption and use by trees (Omoro et al., 2011) and hence play a minor role in the distribution and abundance of tree species (Omoro et al., 2011). In this study, the observation that soil pH did not influence the distribution of abundance of the six species contradicts findings by John et al. (2007) which indicated that soil pH indirectly exerts strong influence on species distributions in tropical forests by influencing the availability of several plant nutrients. In this case, the soil pH did not exert strong influence on the nutrients required for the growth of the six species. Despite the fact that phosphorus is the nutrient that limits the growth of trees and other plants in tropical forests (Vitousek, 1984; Wright et al., 2011; Omoro et al., 2011), the distribution and abundance of the six dominant and adaptable tree species was not affected by this particular soil variable. There is evidence in the literature that phosphorus availability in Afromontane forests in the tropics can be low and declines with elevation (Tanner et al., 1998; Benner et al., 2010). However, efficient cycling of phosphorus through higher resorption efficiency of phosphorus as the plants tissues senesce makes the nutrient available to the plants in sufficient quantities (Dalling et al., 2016). The six species seems to have inherent mechanisms that enhance efficient cycling of phosphorus increasing phosphorus available to them. As a result, the distribution and abundance of the species were not affected by the limitation of phosphorus observed in the fragmented forests of Taita Hills.

4.3. Interaction between most abundant tree species and environmental variables

Unlike the six dominant and adaptable species whose abundance was mainly influenced by the distance from the forest edge, electrical conductivity, potassium and soil moisture, the probability of occurrence of the thirty tree species categorized as most abundant (six dominant and adaptable species included) was mainly influenced by the distance from forest edge, potassium and soil pH. Besides, EC, nitrogen, phosphorus and organic carbon marginally affected the probability of occurrence of the most abundant tree species. Soil moisture did not affect distribution and abundance of most abundant trees species. The distance from the forest edge influenced distribution and abundance of 36.7% of the species classified as most abundant species followed by potassium (23.3%), soil pH (20.0%), phosphorus (6.7%) and organic carbon (3.3%). The EC and nitrogen collectively accounted for 6.7% of species distribution and abundance for the most abundant tree species. The distribution and abundance of the remaining 3.3% of the most abundant species was not dependent either on any of the environmental variables studied or the distance along forest edge-interior gradient. This is consistent with findings of Gruszczynska et al. (1991), Vitousek et al. (1996) and Omoro et al. (2011), which indicated that soil variables are not the only abiotic factors that affect spatial differentiation of plant communities; instead, other factors such as geologic and anthropogenic activities influence the spatial abundance of plant species.

The distance along forest edge-interior greatly influenced the distribution and abundance of most abundant species and this was mainly due to the edge effects (Bennett and Saunders, 2010; Magnago et al., 2015). Moreover, tree species are habitually associated with soils that differ in several physical, chemical and biotic properties (Ayres et al., 2009) and these soil properties vary along forest edge-interior gradient (Bergès et al., 2013). Previous studies have shown that there is a sturdy correlation between potassium and woody species distribution and abundance in tropical forests (Tripler et al., 2006). Moreover, phosphorus is a critical nutrient that limits the growth of forest plants in tropical forests and hence strongly affects tree species distribution and abundance (Vitousek, 1984; Baribault et al., 2012; Li et al., 2013; Dalling et al., 2016). Other related studies have also revealed that soil pH level that increases phosphorus availability promotes the co-existence of tree species affecting their distribution and abundance within a forest community (Xu et al., 2016). Therefore, the large variation in soil properties and ecological functioning along the forest edge-interior gradient explains the great influence of distance from forest edge on species distribution.

The results of this study indicate that organic carbon, EC and nitrogen did not affect the distribution and abundance of the most abundant tree species. This is because soil organic carbon and nitrogen are typically adequate in tropical forests and hence play a minor role in the distribution and abundance of tree species (Omoro et al., 2011). Similarly, EC did not affect the distribution and abundance of most abundant tree species because the values were within the normal range required by plants for successive growth. Studies on interaction between EC and species distribution and abundance in the tropics are rare and therefore we could not find related research findings to allow us make comparison with the present results.

The distribution and abundance of a small proportion of most abundant species (3.3%) was not affected by both environmental variables and the distance from forest edge. Therefore, other factors such as geodynamic and anthropogenic activities may have affected the spatial distribution and occurrence of these particular species (Gruszczynska et al., 1991; Vitousek et al., 1996).

4.4. Interaction between less abundant tree species and environmental variables

This study revealed that the occurrence of eleven tree species categorized as less abundant was majorly affected by organic carbon, EC, soil pH, nitrogen, phosphorus and distance from forest edge. Soil moisture and potassium marginally affected the occurrence of less abundant species. Distance from the forest edge, organic carbon and EC affected the distribution and abundance of 36.4% of the less abundant species. Similarly, soil pH affected the distribution and abundance of 36.4% of the less abundant species. Nitrogen and phosphorus affected the distribution and abundance of 18.2% of the less abundant species while soil moisture and potassium were collectively responsible for the occurrence of 9.1% of the less abundant species. Clearly, the distribution and abundance of the less abundant species was not dependent on only one specific environmental variable but rather on a combination of either two or more variables (Aerts et al., 2006; Laurance, 2007). This is in contrast with most abundant tree species whose distribution and abundance were mostly dependent on one environmental variable. Therefore, interactions among various environmental variables are very important in maintaining the diversity of less abundant tree species in the fragmented forests of Taita Hills.

4.5. Implications on management of fragmented forests

The results of this study highlight the fact that soils on the edges of Taita Hills' forest fragments are of low fertility, and have low moisture content. These factors are likely to be strongly limiting natural regeneration of indigenous species at the forest edges (Benitez-Malvido, 1998; Bruna, 1999) and hence reducing species richness and diversity (Kacholi, 2014). Moreover, moisture-stressed trees on the forest edges shed leaves, and because of drier edge conditions, the rate of litter decomposition is slow (Didham, 1998). Accumulating litter affects seed germination (Bruna, 1999) and seedlings survival (Scariot, 2001) and makes forest edges vulnerable to surface fires during droughts (Cochrane et al., 1999). Under such conditions, establishment of agroforestry belts on the boundaries of the forest fragments to ameliorate the adversarial microclimatic conditions created on the forest edges due to the edge effect is likely to be a wiser management strategy from a long-term perspective. The amelioration of micro-climatic conditions on the forest edges can create favourable conditions for secondary forest growth and hence enhancing resilience of the forest fragments to the edge effects and conserving the remaining biodiversity.

The distribution and abundance of tree species were mainly influenced by distance from the forest edge, soil moisture, nitrogen, EC and potassium. The knowledge on the relationships between the five environmental variables and tree species should be utilized in developing effective restoration strategies able to produce self-sustaining forests that promotes biodiversity conservation and ecosystem function (Gibson et al., 2011; Magnago et al., 2014). This is because successful restoration activities are based on solid scientific information (Rodrigues et al., 2009). Besides, soil properties-tree species relationships established in this study should be used in selecting suitable native species for restoration programmes (Omoro et al., 2011). The Taita Hills forest fragments are moderately-heavily disturbed with heavy presence of gaps (Omoro et al., 2010, 2011; Wekesa et al., 2016), and therefore, planting of suitable tree species, well adapted to particular soil conditions is likely to facilitate and accelerate recovery of degraded sites within the forest fragments leading to rapid successional development.

5. Conclusions

This study tested the hypotheses that environmental variables (soil moisture, organic carbon, phosphorus, soil pH, electrical conductivity, nitrogen and potassium) are different on the forest edge, intermediate forest and forest interior, and that the distribution and abundance of tree species reflects the changes in environmental variables along forest edge-interior gradient. The edge effect greatly influenced environmental variables along forest edge-interior gradient. The environmental variables interacted with one another and with distance from the forest edge and the interactions influenced the distribution and abundance of tree species along the forest-edge-interior gradient. The distribution and abundance of six dominant and adaptable species (*M. conglomerata*, *A. gummifera*, *S. guineense*, *X. monospora*, *T. stapfiana* and *M. lanceolata*) were mainly influenced by distance from the forest edge, EC, potassium and soil moisture. Moreover, the distribution and abundance of the other tree species (six dominant and adaptable species excluded) was mainly influenced by nitrogen, EC, the distance from forest edge and soil pH. Overall, distance from the forest edge, soil moisture, nitrogen, EC and potassium were the key environmental variables that determined species distribution and abundance in forest fragments of Taita Hills. Therefore, restoration efforts including enrichment planting should take into consideration the relationships between environmental variables and tree species in selecting suitable and better adapted species for optimal establishment, survival and growth of planted seedlings to enhance recovery.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.12.023.

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