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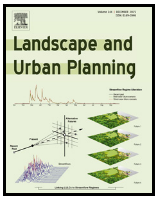

Research paper

Trees in a human-modified tropical landscape: Species and trait composition and potential ecosystem services

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HIGHLIGHTS

- Several tree traits are non-random distributed in the human-dominated landscape.
- Exotic fruit trees were more abundant on croplands.
- Three functional traits were associated with exotic species.
- Indigenous trees species were abundant on wooded sites and homesteads.
- No functional traits were exclusively associated with indigenous species.

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ABSTRACT

Worldwide, large areas of the tropics are transformed into simplified ecosystems characterised by altered tree species composition and diversity. Human activities in these landscapes have a strong effect on the land cover and exert a selective force on tree species and functional traits, hereby potentially shaping the distribution of ecosystem services in the landscape. The aim of this study was to asses how the land use determines tree species assemblages, their associated traits and potential ecosystem services, which was studied for 589 systematically sampled locations in the Afromontane highlands of Taita Hills (SE Kenya). Several tree traits were non-random distributed in the human-dominated landscape. For instance, on croplands (70% of the sampled locations) belonged 66.5% of the observed species to the exotic tree species group. This group was characterised by significantly larger seeds and fruits, corresponding with the abundance of many fruit trees. Also three functional traits (i.e. economic function, nitrogen fixation and agroforestry potential) were clearly associated with this group. The cloud forest tree species group and small-leaved indigenous group were significantly more present on woodes sites and homesteads (~42%). However, no functional traits were unique for both indigenous groups, implying that farmers may exchange them by exotics, which could be catalysed by the loss of local knowledge about indigenous tree resources and benefits. Other indigenous species, including endemic or late-successional species were rare or absent in the matrix and their conservation can only be guaranteed by protecting the remaining indigenous forest fragments.

1. Introduction

The human population growth causes a rising demand for resources, including food, fibber and fuel, which induces conversion of indigenous forests to agricultural fields, exotic tree plantations and settlements (Carreño-Rocabado et al., 2012; Ellis, Antill, & Kreft, 2012; Hilderbrand, Watts, & Randle, 2005; Norris

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et al., 2010; Pellikka et al., 2013). Research in deforested landscapes has so far mainly focused on the indigenous forest relicts. This has contributed to the perception of a segregated landscape with two apparently independent and conflicting entities, namely the forest relicts as biodiversity refuges and the irrelevant matrix (Carreño-Rocabado et al., 2012; Perfecto & Vandermeer, 2008). However, there is growing consensus that these landscapes do not consist of independent entities, but have ecologically interacting components (Burel et al., 2013; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014). For instance, trees in the matrix may function as stepping stones or dispersal foci for many forest plants, as seeds accumulate under their canopies after visitation by forest frugivores (Herrera & Garcia, 2010). This implies that the future of tropical forest biodiversity not only depends on an effective management of the indigenous forest relicts, but of the complete landscape (DeClerck et al., 2010; Gardner et al., 2009; Perfecto & Vandermeer, 2008).

Remnant trees, i.e. isolated scattered trees persisting in a matrix originally occupied by forest, as well as isolated planted trees are common features in many human-modified forest landscapes worldwide (Herrera & Garcia, 2009; Manning, Fischer, & Lindenmayer, 2006). Their occurrence is strongly influenced by human interventions in the landscape (Metzger, 2000). First, direct interventions favour useful (e.g. nutritious, medicinal or ornamental) tree species in homegardens, agricultural fields or managed forests to provide goods and services (Burkhard, Kroll, Nedkov, & Muller, 2012; DeClerck et al., 2010). Second, non-forested areas have largely lost the shaded and tempered forest microclimate, are inaccessible to species of low dispersal capacity and have high levels of seed predation and seedling herbivory, which may catalyse extinction of indigenous species and invasion of exotic species (DeClerck et al., 2010; Metzger, 2000). Especially shade-tolerant species and species with zoochorous and barochorous seed dispersal appear to be more strongly influenced by habitat modifications. Species composition changes may result in a reduction or loss of ecosystem services such as carbon storage and sequestration, although it is recognised that converted land can also provide substantial ecosystem services (Barrett, Valentim, & Turner, 2013; Douglas et al., 2013). For instance, leguminous trees in farmland may provide valuable ecosystem services such as nitrogen fixation and fuelwood production, which can enhance agricultural productivity and income. Therefore, a better understanding of the benefits of remnant or scattered trees is essential for developing effective management options, particularly within tropical regions with intense land use pressure.

Here, the results of a landscape, tree species and trait composition study from the Taita Hills in south-east Kenya are presented. This study comprised agricultural fields, exotic tree plantations, urban settlements, rocky areas and indigenous Afromontane cloud forest relicts. The objectives of the study were to asses whether differences in landscape configuration (e.g. land cover composition and distance to indigenous forest or town) in a deforested and human-modified landscape are reflected in tree species and trait occurrence and their potential ecosystem services. It was hypothesised that: (1) there is a non-random distribution of tree traits in the landscape; (2) the density of trees with multiple provisioning services (i.e. food, fodder, firewood) is higher in the neighbourhood of areas with higher human activity; (3) exotic tree species provide different services than indigenous tree species and these traits are more economically valorised.

2. Materials and methods

2.1. Study area

The Taita Hills Afromontane cloud forests (south-east Kenya – 3°20′S, 38°15′E –Fig. 1a) form the northernmost component of the Eastern Arc Mountains, which are known as a biodiversity hotspot (Burgess et al., 2007). The forests are home to many endemic and endangered forest dependent species (e.g. *Dorstenia christenhuszii*, *Coffea fadenii*) (Chase, Thijs, Kamau, & Fay, 2013; Thijs et al., 2014a). Archaeological research revealed that the clearance of these forests started about 2300 BC, with a deforestation peak during the last 200 years due to a rapid population growth (Hildebrandt, 1877; Pellikka, Lotjonen, Sijander, & Lens, 2009; Schmidt, 1989). Currently, only 440 ha of indigenous forest persists in 12 forest relicts, of which 9 are smaller than 10 ha (Aerts et al., 2011; Beentje & Ddiang'ui, 1988; Pellikka et al., 2009). The agricultural activities in the area are characterised by small-scale subsistence farming (e.g. maize, banana, beans, cassava; farm size: 0.16–4 ha) and supplementary irrigation practice is common because rainfall is too erratic to ensure stable production. A study area of 19 km^2 was defined in the centre of Taita Hills (Fig. 1b), because it is crucial to increase landscape connectivity and it is therefore recognised as a target area for rehabilitation (Adriaensen, Githiru, Matthysen, & Lens, 2006). This study provides pertinent information and data to other projects whose main outcome would be a model on forest connectivity of the Taita Hills (Aben et al., 2012; Githiru, Lens, Adriaensen, Mwang'ombe, & Matthysen, 2011; Lens, Van Dongen, Norris, Githiru, & Matthysen, 2002).

2.2. Land cover composition

Within the study area, 589 sample points were systematically sampled along 25 east-west oriented transect lines. The distance between transect lines and between individual sample points was 200 and 150 m, respectively. At each location, the elevation was determined with a GPS (Garmin GPSmap 60CSx) at the plot centre. Subsequently, the land cover composition was determined in a circular plot (sample point as centre, radius 50 m) using the Land Cover Classification System (LCCS) of the Food and Agriculture Organization of the United Nations (FAO) and the United Nations Environment Programme (UNEP) (Di Gregorio, 2005). Spatial variables were calculated in as the horizontal distance from the plot centre to the edge of the nearest element of indigenous forest, road, house and town (i.e. cluster of houses with one or more shops, often at the intersection of roads). Spatial data analysis was performed in ArcGIS 9.2 (ESRI, Redlands, CA).

2.3. Tree species composition

At each sample point, an inventory of the mature trees (woody individual ≥5 m) was performed by plotless (i.e. distance-based) sampling, because the density of trees in the matrix was too low for convenient quadrat sampling. Therefore, the Byth robust T-square density estimator (Fig. 2) was used: $D_{\text{TSB}} = 1/\left(2 \cdot \sqrt{2} \cdot x_1 \cdot x_2\right)$, where D_{TSB} is the tree density (stems per ha), x_1 the distance (m) from the sample point (SP) to the closest (CI) tree and x_2 the distance (m) from the CI to its nearest neighbour tree (NN), occurring in the half-plane at the far side of the line through the CI that is perpendicular to the line from the SP to the CI (Engeman, Sugihara, Pank, & Dusenberry, 1994). Every specimen was identified according to the nomenclature of the Flora of Tropical East Africa; the diameter at breast height (DBH) and tree height were measured for each individual.

2.4. Tree species traits

Trait data was collected for each recorded species, based on published floras and databases, herbarium records (East African Herbarium, Kenya) and field observations (Appendices A and B). We focused on five groups of traits (Table 1): (i) Biogeographical traits comprise the species natural distribution (Dorrough &

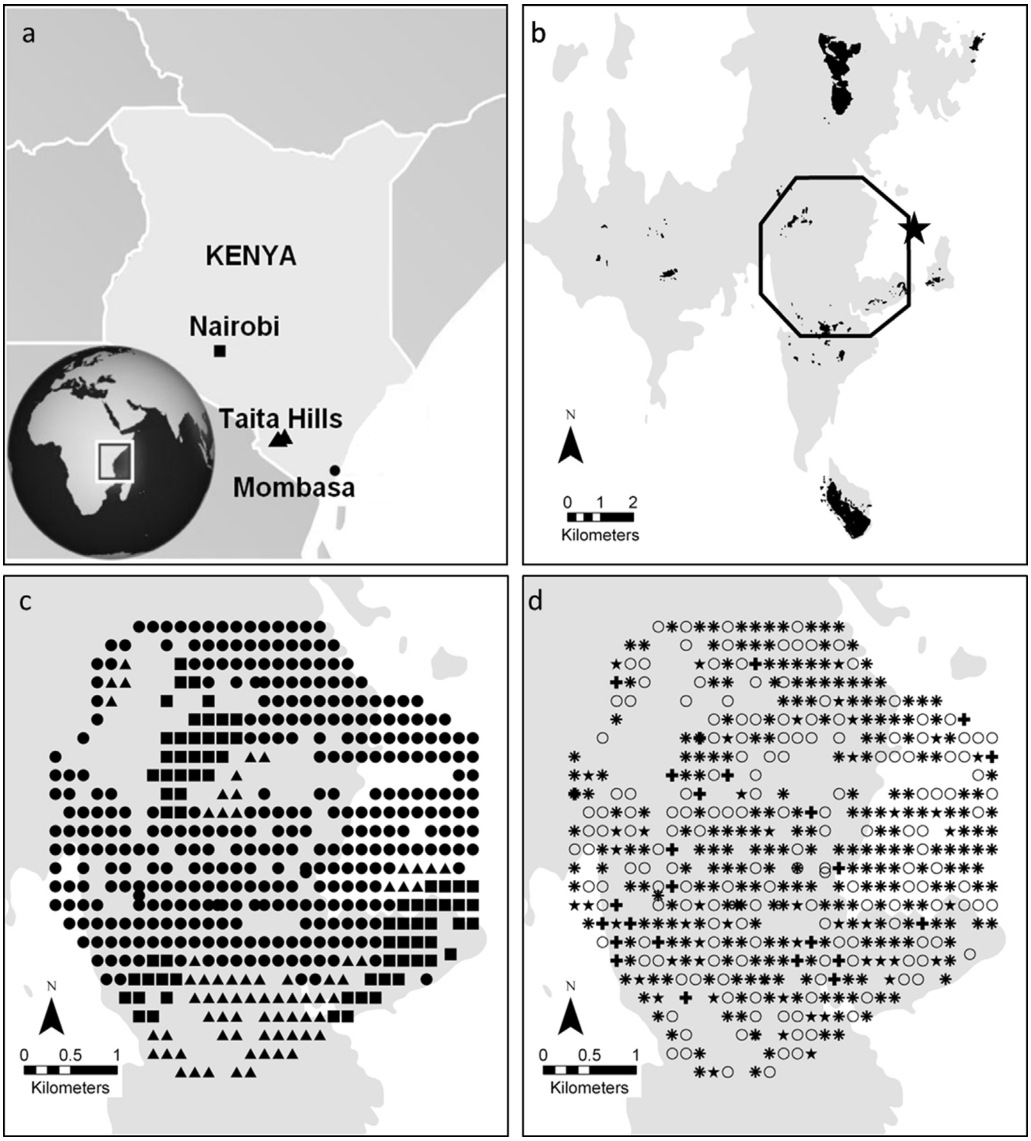

Fig. 1. (a) The geographical position of the Taita Hills in Kenya; (b) Position of the study area (octagon) in the Taita Hills, the grey area is at 1500 m asl or higher, the black polygons are the remaining indigenous forest relicts and the star represents Wundanyi, the administrative centre of the Taita-Taveta District; (c) Within the study area, the landcover cover composition was determined in 589 sample points and three distinctive landscape types were defined: wooded sites (■), homesteads (▲) and croplands (●); (d) For each sample point was determined which emergent functional tree species group dominated: Cloud forest tree species group (★), small-leaved indigenous tree species group (✚) and economic valuable exotic group (✱). A circle was used (○) when species of more than one emergent functional tree species group occurred in a sample point.

Scroggie, 2008). (ii) Reproduction traits comprise pollination systems, seed and fruit types and seed dispersal system (Burkhard et al., 2012; Girão, Lopes, Tabarelli, & Bruna, 2007; Katovai, Burley, & Mayfield, 2012; Mayfield, Ackerly, & Daily, 2006; Metzger, 2000; Roscher et al., 2004). (iii) Morphological traits describe plant architecture and define space occupancy (Roscher et al., 2004). (iv) Phenological traits describe plant development, temporal presence and toxicity (Flynn et al., 2009; Metzger, 2000; Roscher et al., 2004). (v) Functional traits refer to the potential of a particular tree species to provide ecosystem services. In this study, it comprises a specific bundle of provisioning (e.g. timber, animal fodder), regulating (e.g. nitrogen fixation, erosion control), and cultural services (e.g. ornamental use, conservation value) (Burkhard et al., 2012; DeClerck et al., 2010; Flynn et al., 2009; Roscher et al., 2004). In this study, 25 traits were used and the categorical traits pollination type, seed dispersal and shade tolerance were converted to binary traits, resulting in 31 traits that were used in further data analysis.

2.5. Data analysis

2.5.1. Landscape type and emergent functional tree group delineation

A Principal Component Analysis (PCA) was used to determine the main environmental gradients in the landscape data (i.e. five land cover and four spatial variables). The 589 sample points were clustered into landscape types using Sørensen distance with flexible beta linkage $\beta = -0.25$ (McCune & Mefford, 2002). A multi-response permutation procedure test (MRPP) was used to test for multivariate differences in landscape characteristics among the defined landscape types. For MRPP, the Sørensen distance measure and a natural group weighting factor $n_i/\Sigma n_i$ were used, where n_i is the number of sample plots in each group. The test statistic, T, describes the separation between groups while the chance-corrected within-group agreement, A, describes within-group homogeneity compared to random expectation (McCune & Mefford, 2002). To test for concordance between the landscape

Table 1
Distribution of tree species traits of remnant trees ($n = 1178$) in the Taita Hills, as sampled by the Byth robust T-square plotless sampling. The relative proportion of species within each trait is given in parentheses. More information of some traits, which are marked with an asterix, is provided in the footnote.

Biogeographical traits		Morphological traits	
Plant origin	Cloud forest species	Maximum tree height*	Leaf area*
Exotic (40.0) Indigenous (60.0)	Yes (42.0) No (58.0)	Tiny (29.1) Small (36.0) Medium (18.6) Large (16.3)	Tiny (35.6) Small (27.6) Medium (26.5) Large (10.3)

Reproduction traits					
Pollination	Seed size*	Fruit size*	Fruit type	Seed dispersal	Capacity for clonal growth
Insect (88.6) Bird (5.7) Wind (5.7)	Tiny (18.3) Small (32.8) Medium (28.2) Large (20.7)	Tiny (6.9) Small (11.5) Medium (28.7) Large (52.9)	Fleshy (58.0) Non-fleshy (42.0)	Anemochory (22.7) Zoochory (64.8) Barochory (12.5)	Yes (12.5) No (87.5)

Phenological traits		
Foliage persistence	Shade tolerance	Toxicity
Evergreen (46.6) Deciduous (53.4)	Tolerant (18.0) Intermediate-tolerant (40.0) Intolerant (42.0)	Yes (17.0) No (83.0)

Functional traits (potential to provide ecosystem services)					
Provisioning services					
Edible plant parts	Animal fodder	Timber	Energy provision	Biochemicals and medicinals	Economic importance*
Yes (83.3) No (16.7)	Yes (44.3) No (55.7)	Yes (53.4) No (46.6)	Yes (44.3) No (55.7)	Yes (71.6) No (28.4)	Yes (33.0) No (67.0)

Regulating services			
Erosion control	Nutrient regulating	Nitrogen fixation	Agroforestry use
Yes (22.7) No (77.3)	Yes (23.9) No (76.1)	Yes (10.2) No (89.8)	Yes (18.2) No (81.8)

Cultural services	
Conservation value*	Ornamental use
Yes (5.7) No (94.3)	Yes (2.3) No (97.7)

* Maximum tree height is the maximum height (m) that a tree species can grow: tiny ≤ 5; $5 <$ small ≤ 15 m; $15 <$ medium ≤ 25 m; large > 25 m). Leaf area (cm^2): tiny ≤ 50; $50 <$ small ≤ 100; $100 <$ medium ≤ 250; $250 <$ large ≤ 1000; huge > 1000. Seed size is the length of the seed (mm): tiny ≤ 1; $1 <$ small ≤ 3; $3 <$ medium–small ≤ 8; $8 <$ medium ≤ 12; large > 12. Fruit size is the length of the fruit: tiny ≤ 2; $2 <$ small ≤ 5; $5 <$ medium ≤ 15; large > 15. Economic importance: trees that produce products or services that are marketable. Conservation value: endemic and/or climax species are defined as threathened species, needing specific conservation measures.

variables and the PCA dimensions, Spearman rank correlation coefficients (r_s) were calculated and evaluated. For each landscape variable, differences among landscape types were analysed using non-parametric Kruskal–Wallis tests (KW) for continuous data and Chi-square test (χ^2) for binary data with a Bonferroni correction for multiple comparisons. Pair-wise comparisons were calculated with Mann–Whitney U tests for continuous data or Chi-square tests for categorical data.

Through a similar approach as the landscape type delineation emergent functional tree groups were defined based on the tree trait data. The two biogeographical traits (i.e. plant origin and cloud forest species) were not included in this analysis, thus they did not contribute to the delimitation of the emergent functional tree group delineation. Chi-square tests were used to test for differences between the emergent functional tree groups for the number of indigenous species and cloud forest species. Subsequently the number of trees for each emergent functional tree group per sample point was determined.

2.5.2. Landscape vs trees

Two approaches were used to link the landscape configuration with the distribution of tree traits in the landscape. The first analysis tested if there is a non-random distribution of the tree traits in the landscape by using a Mantel correlation test on two Gower distance matrices, one based on the landscape characteristics and the other on the tree trait profiles at each sample point. The second analysis tested if the representation of each emergent functional tree group differed across the different landscape types. Therefore a non-parametric Kruskal–Wallis test was used with landscape type as independent variable and the number of trees per emergent functional tree group as dependent variable. MRPP, ordination and classification analyses were carried out in PC-ORD 6 (McCune & Mefford, 2002), distance matrices and correlation coefficients were calculated with the package 'ecodist' in R 3.0.1, other statistical tests were performed in SPSS 20 (IBM, 2011).

3. Results

3.1. Land cover composition and landscape type delineation

The study area consisted of 74.8% cultivated area, 13.3% urban settlement, 9.8% exotic tree plantations, 1.3% rocky area and 0.8% indigenous Afromontane cloud forest. The PCA ordination and cluster analysis on landscape variables resulted in three distinct

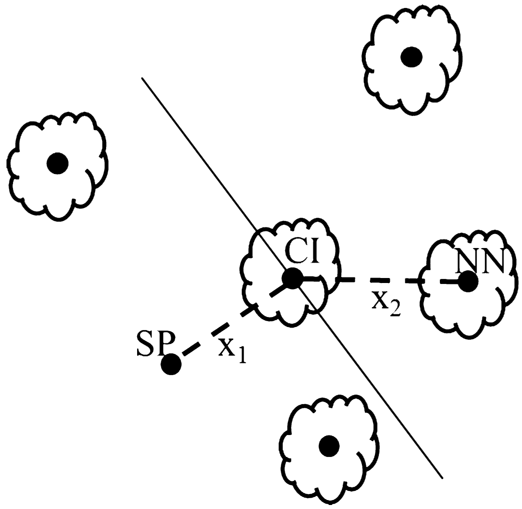

Fig. 2. The *T*-square plotless sampling method. SP = sample point, CI = closest tree from SP; NN = nearest neighbour tree of CI on the far side of the line (—) perpendicular to the line SP-CI; x_1 = the distance from SP to CI; x_2 = the distance from CI to NN. Adapted from (Aerts et al., 2006).

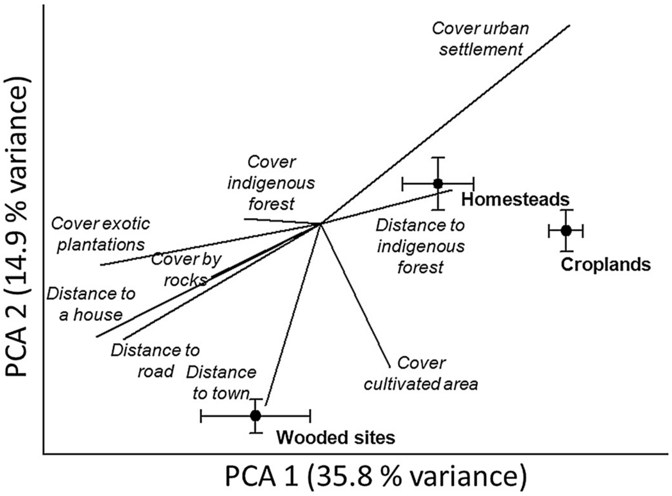

Fig. 3. Joint plot showing the three landscape types and the land cover and spatial variables. The landscape types, resulting from the cluster analysis, are presented by the average and SE of their respective PCA ordination scores. The angle and length of the vectors tell the direction and strength of the relationships of the land cover and spatial variables with the ordination axes. See Appendix A for Spearman rank correlation scores.

landscape types, which could be interpreted as ‘wooded site’, ‘cropland’ and ‘homestead’ ($A = 0.12$; $T = -81.37$; $P < 0.001$) (Figs. 3 and 4; Table 2; Appendix C). *Wooded sites* were charachterised by a high exotic tree canopy cover ($\chi^2 = 14.34$, $P = 0.001$) and low cover by urban settlement ($\chi^2 = 10.97$, $P = 0.002$). Wooded sites were located on higher altitudes ($\chi^2 = 14.09$, $P = 0.001$), in the neighbourhood of indigenous forest relicts ($\chi^2 = 305.77$, $P < 0.001$) and far away of towns ($\chi^2 = 122.71$, $P < 0.001$). Wooded sites were characterised by the highest tree density ($\chi^2 = 7.55$, $P = 0.002$), the smallest ($\chi^2 = 6.32$, $P = 0.003$) and thinnest trees ($\chi^2 = 6.82$, $P = 0.001$). *Croplands* were located at lower altitudes ($\chi^2 = 14.09$, $P = 0.001$), had the lowest cover of indigenous forest ($\chi^2 = 15.24$, $P < 0.001$) and

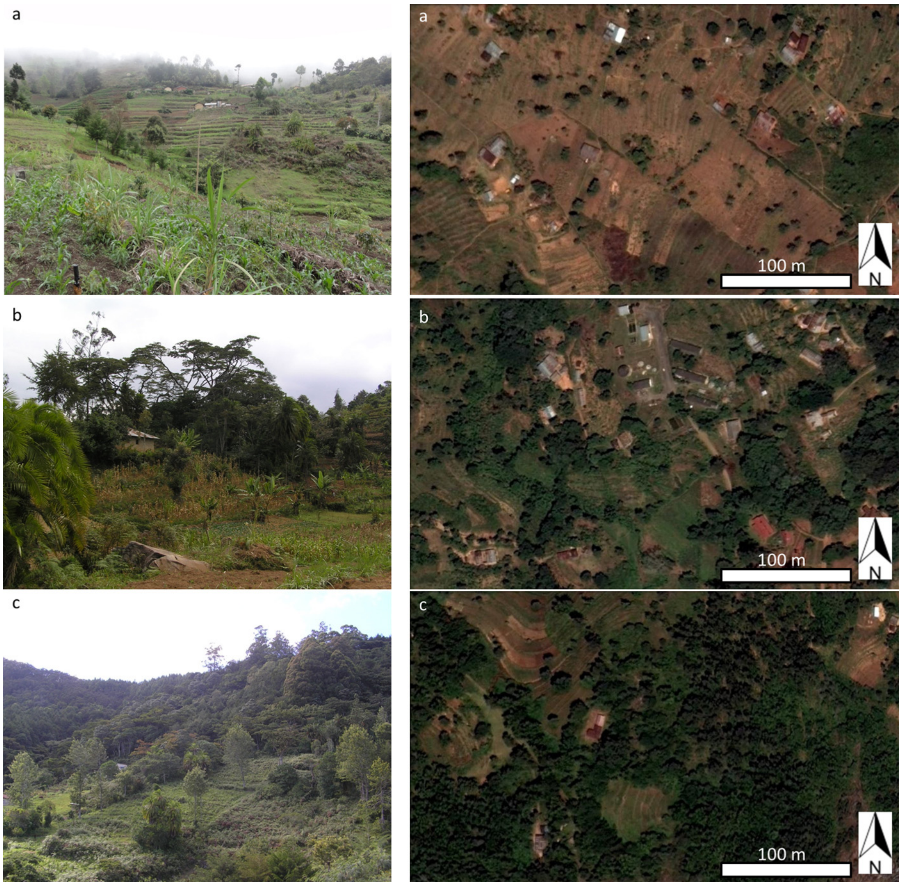

Fig. 4. Photograph and satellite image (© 2013 U.S. Geological Survey, DigitalGlobe & GeoEye by way of Google Earth) of cropland (a), homestead (b) and wooded site (c) in the Taita Hills, southeast Kenya.

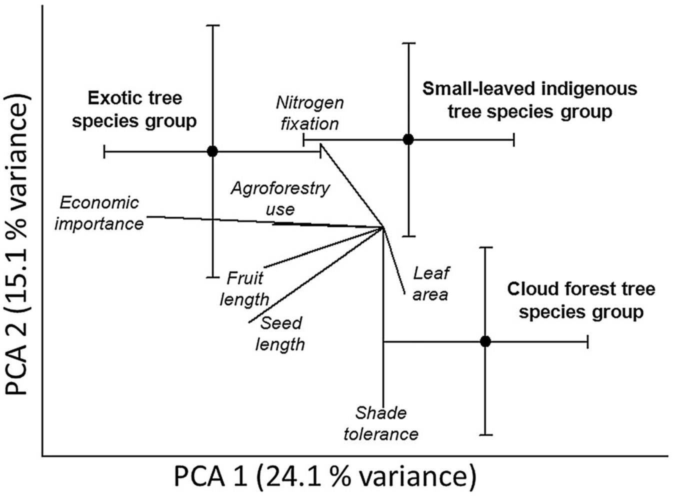

Fig. 5. Joint plot showing the three functional tree groups and the tree traits that significantly differ between the three groups. The functional tree groups, resulting from the cluster analysis, are presented by the average and SE of their respective PCA ordination scores. The angle and length of the vectors tell the direction and strength of the relationships of the land cover and spatial variables with the ordination axes. See Appendix B for Spearman rank correlation scores.

were farthest away from indigenenous forest relicts ($\chi^2 = 305.77$, $P < 0.001$). The characteristics of *homesteads* were often intermediate between these of croplands and wooded sites (e.g. elevation, cover urban settlement, distance to indigenous forest), but they were significantly nearer to towns ($\chi^2 = 122.71$, $P < 0.001$). All three landscape types had the same proportion of cultivated land ($\chi^2 = 4.00$, $P = 0.14$). However, a significantly higher proportion was used as fallow land or forest-plantation in wooded sites than in croplands ($\chi^2 = 15.63$, $P = 0.003$). Within this study area, 70.5% of the sample points could be assigned to cropland, while 15.0% and 14.5% could be assigned to wooded sites and homesteads, respectively (Fig. 1c).

3.2. Tree species and trait composition and funtional tree group delineation

A total of 88 tree species belonging to 55 families were recorded, of which 60% is from indigenous origin and 42% of the observed species can be defined as cloud forest species. The five most common tree species, corresponding with 60% of the recorded specimens, were all exotic species (i.e. *Acacia mearnsii*, *Cupressus lusitanica*, *Eucalyptus saligna*, *Grevillea robusta*, *Persea americana*), while only 2.3% of the species were rare species with a high conservation value (Table 1). The majority of the observed species were insect pollinated (88.6%), had large and fleshy fruits (52.9% and 58.0%) and seeds that are dispersed by animals (64.8%). Most tree species had edible plant parts (83.3%), contained biochemicals (71.6%) or produced timber (53.4%), although these products are only marketable for 33% of the tree species. A minority of the tree species provided regulating services like erosion control (22.7%), nutrient regulating (23.9%), nitrogen fixation (10.2%) or agroforestry potential (18.2%). The PCA ordination and cluster analysis on the tree trait variables resulted in three distinct emergent functional tree groups ($A = 0.25$; $T = -36.91$; $P < 0.001$) (Fig. 5, Table 3, Appendix D). The proportion of indigenous species and cloud forest species differed significantly between the three emergent functional tree groups ($\chi^2 = 23.76$, $P < 0.001$ and $\chi^2 = 12.95$, $P = 0.002$, respectively) (Table 3). The three emergent functional tree groups could be interpreted as '*cloud forest tree species group*', '*small-leaved indigenous tree species group*' and '*exotic tree species group*'. The *cloud forest tree species group* is characterised by a high proportion of indigenous species ($\chi^2 = 23.76$, $P < 0.001$), cloud forest species ($\chi^2 = 12.95$, $P < 0.002$) and shade-tolerant species ($\chi^2 = 6.61$, $P < 0.001$). The trees are characterised by large leaves ($\chi^2 = 36.99$, $P < 0.001$). *Celtis gomphophylla*, *Psychotria petitii* and *Xymalos monospora* are examples of this group. The *small-leaved indigenous tree species group* is characterised by indigenous species ($\chi^2 = 23.76$, $P < 0.001$) with small leaves ($\chi^2 = 36.99$, $P < 0.001$). *Bersama abyssinica*, *Millettia oblate* and *Prunus africana* are three examples. The *exotic tree species group* is characterised by exotic species ($\chi^2 = 23.76$, $P < 0.001$) with large seeds ($\chi^2 = 15.35$, $P < 0.001$), fruits ($\chi^2 = 43.74$, $P < 0.001$) and leaves ($\chi^2 = 36.99$, $P < 0.001$). This group is characterised by their economic function ($\chi^2 = 21.58$, $P < 0.001$), nitrogen fixation ($\chi^2 = 8.77$, $P = 0.001$) and agroforestry use ($\chi^2 = 6.85$, $P = 0.001$). *Carica papaya*, *A. mearnsii* and *G. robusta* are some well-known species from this group. In the study area, 64% of the observed individuals were from the exotic tree species group, while 22% and 14% could be assigned to the cloud forest tree species group and small-leaved indigenous tree species group, respectively (Fig. 1d).

3.3. Landscape vs trees

Differences in tree traits followed differences in land use and spatial structure, i.e. there were multivariate similarities among landscape structure and tree traits (Mantel $r = -0.04$, $P = 0.047$). The cloud forest tree species group occurred significantly more in the wooded sites than in the croplands ($\chi^2 = 9.75$, $P = 0.008$). In contrast, the exotic tree species group occurred significantly more in the croplands than in de wooded sites ($\chi^2 = 5.44$, $P = 0.046$) (Table 4). For the small-leaved indigenous tree species group was no difference observed between the three landscape types ($\chi^2 = 1.06$, $P = 0.588$) and no differences were found between wooded sites and homesteads for the three emergent functional tree groups.

4. Discussion

Our results support the hypothesis that there is a non-random distribution of tree traits in the landscape. Dependent on the location within the human-dominated landscape, other tree traits can be expected. This is not surprising, direct or indirect human interventions in the landscape may favour specific tree traits. However, this effect was found for nine tree traits, while the occurrence of the other 16 tree traits could not be differentiated between the different landscape types (see Table 3). This explains why we found a significant, but weak correlation between the landscape characteristics and tree traits, because all tree traits were included in the Mantel test.

Several specific ecosystem services are more common in the neighbourhood of places with more human activity. Human activity occurs inherently and area-wide in the human dominated landscape where circa 98% of the land cover is non-natural (i.e. $\sim$75% cultivated area, $\sim$13% urban settlement and $\sim$10% exotic tree plantations) (Gardner, Barlow, Sodhi, & Peres, 2010). Human activity (i.e. cattle browsing and logging) even occurs in the indigenous Afromontane forest relicts ($\sim$1% of the study area) (Thijs et al., 2014a). The intensity of human activity must be the lowest in wooded sites, which were characterised by a low cover of urban settlement, larger distance to towns and higher proportions of non labour-intensive land uses as fallow land and forest plantations. In contrast, the highest activity is expected on the croplands. The representation of the three emergent functional tree species groups differed between these croplands and the other two landscape types (i.e. wooded sites and homesteads), where significantly more trees of the exotic tree species group occurred. In contrast with the other emergent functional tree groups, this group was

Table 2
The land cover, spatial and stand structural variables (mean ± SE) of wooded sites, homesteads and croplands. For continuous data, the non-parametric Kruskal–Wallis test is used, the average ± SE is presented. For other data, he Chi-square test is used, and the relative distribution (%) between the three functional groups is presented. A corrected $\alpha_{corr} = 0.0031$ was used to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for 16 tests). Pairwise differences are indicated by different letters.

	Wooded sites		Homesteads		Croplands			
	Mean	SE	Mean	SE	Mean	SE	χ^2	*P*
Site characteristics								
Elevation (m asl)	1659.55 a	18.37	1602.21 b	10.82	1575.50 b	6.84	14.09	0.001
Land cover (relative proportion) (%)								
Cultivated area	72.95	1.84	77.60	1.56	74.66	0.89	4.00	0.135
Exotic tree cover	15.66 a	2.11	8.06 b	1.29	8.87 b	0.31	14.34	0.001
Indigenous tree cover	1.58 a	0.66	2.40 a	0.87	0.31 b	0.12	15.24	<0.001
Urban settlement	8.36 a	0.78	11.53 b	1.045	14.69 b	1.47	10.97	0.002
Rocky area	1.45	0.59	0.41	0.31	1.47	0.24	6.50	0.004
Distance (m)								
Indigenous forest	372.92 a	18.01	537.84 b	23.84	1303.95 c	20.22	305.77	<0.001
Town	904.25 a	18.05	370.41 b	17.50	793.80 c	17.57	122.71	<0.001
House	50.75	5.48	48.26	4.53	42.16	1.69	1.59	0.45
Road	69.92	7.40	55.05	5.34	58.22	3.06	2.29	0.319
Landover classification system							Chi^2 test	
Cover of cultivated land (%)[a]	63.2/30.2/6.6 a		49.3/46.5/4.1 ab		46.5/51.8/1.7 b		15.63	0.003
Cover of permanent life forms (%)[b]	5.3/61.8/32.9 a		1.4/30.3/38.4 a		0.3/47.3/52.4 b		23.52	<0.001
Stand structural characteristics								
Density (#/ha)	268 a	42.16	230 ab	20.79	196 b	29.36	7.55	0.002
Cover (%)	27.50 a	1.73	21.37 b	1.45	19.37 b	0.57	20.60	<0.001
Height (m)	9.95 a	0.41	11.22 b	0.47	11.36 b	0.26	6.32	0.003
Diameter (m)	0.16 a	0.06	0.19 b	0.06	0.19 b	0.05	6.82	0.001

[a] Each cell shows the proportion of fallow/permanent/forest-plantation cover within the cultivated land for the respective site type. *Fallow*: agricultural system with an alternation between a cropping period of several years and a fallow period, *permanent*: crops that are not replanted for several years after each harvest (e.g. bananas, sugar cane, grasses), *forest-plantation*: like permanent, but with trees and shrubs.

[b] Each cell shows the proportion of closed/open/sparse cover of permanent life forms for the respective site type. *Closed*: ≥ 70%, *open*: > 20 and < 70%, *sparse*: ≤ 20%.

Table 3
Species tree traits that are significantly different between the three emergent functional tree groups. For continuous data, the non-parametric Kruskal–Wallis test is used and the average ± SE is presented. For binary data, the Chi-square test is used and the proportion (%) of species having the specific trait within the emergent functional tree group is presented. A corrected $\alpha_{corr} = 0.0017$ was used to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for 29 tests). Pairwise differences are indicated by different letters.

	Cloud forest tree species group		Small-leaved indigenous tree species group		Exotic tree species group			
	Mean	SE	Mean	SE	Mean	SE	χ^2	*P*
Seed length	6.81 a	1.12	4.05 a	0.57	18.69 b	4.94	15.35	<0.001
Fruit length	14.51 a	2.02	13.20 a	2.39	113.69 b	13.97	43.74	<0.001
Leaf area	110.87 a	10.93	23.20 b	3.22	578.82 a	193.31	36.99	<0.001
							Chi^2 test	
Economic importance[*]	16.7 a		20.0 a		69.2 b		21.58	<0.001
Nitrogen fixation[*]	0.00 a		12.0 b		23.1 c		8.77	0.001
Agroforestry use[*]	13.9 a		8.0 a		34.6 b		6.85	0.001
Shade tolerant	30.6 a		8.0 b		11.5 b		6.61	<0.001
Plant origin[*]	16.7 a		32.0 b		76.9 c		23.76	<0.001
Cloud forest species[*]	61.1 a		44.0 a		15.4 c		12.95	0.002

[*] Economic importance: a higher value indicates that the functional group has a higher proportion of threes that produce marketable products and services. Nitrogen fixation: idem, but more nitrogen-fixating trees. Agroforestry use: idem, but more trees that can function in an agroforestry system. Plant origin: idem, but more trees that are from exotic origin. Cloud forest species: idem, but more trees that can be characterised as cloud forest species.

characterised by a higher occurrence of three ecosystem services: (i) the potential to deliver marketable products or services, (ii) nitrogen fixation and (iii) the potential to be used in agroforestry systems. First, trees of the exotic tree species group can deliver marketable products or services. The seed and fruit length for trees of this group is significantly larger than for the other groups, and the large size corresponds with the many fruit trees in this group, like *Carica papaya*, *Casimiroa edulis*, *Eriobotrya japonica*, *Mangifera*

Table 4
Distribution of the three emergent functional tree species groups between the three landscape types. The non-parametric Kruskal–Wallis test is used and the average ± SE is presented. Pairwise differences are indicated by different letters.

Emergent functional tree species group	Homesteads		Wooded sites		Croplands		Kruskal–Wallis	
	Mean	SE	Mean	SE	Mean	SE		
Cloud forest tree species group	23.0 ab	3.80	32.0 a	4.40	19.0 b	1.75	9.75	0.008
Small-leaved indigenous tree species group	18.0	3.60	11.5	2.50	14.5	1.50	1.06	0.588
Exotic tree species group	59.0 ab	4.65	56.5 a	4.95	66.5 b	2.15	5.44	0.046

indica, *P. americana* or *Psidium guajava*. Trees with large seeds were expected to occur in low numbers in the matrix (Jesus, Pivello, Meirelles, Franco, & Metzger, 2012; Moran, Catterall, & Kanowski, 2009), but we were not able to confirm this result due to the dominance of (exotic) tree species with large fruits in our study area. Another marketable product is timberwood, which is provided by typical species like *A. mearnsii*, *C. lusitanica*, *G. robusta* or *Pinus patula*, which are widely used in tropical plantations (Thijs et al., 2014b). Beside trees with marketable products, nitrogen-fixing trees are a common feature in croplands. Many tropical soils lack soil nitrogen and fertilisers are required to address low yields and thus low income. However, agriculture in many tropical regions is characterised by smallholder farming on a few hectares of land, where financial resources are lacking to apply fertilisers (Leakey, 2014). The presence of nitrogen-fixing trees (i.e. the biological conversion of atmospheric dinitrogen into mineral N by trees) on the croplands is a clear indication that the local farmers make use of these trees as cheap alternative for commercial N fertilisers, besides their other properties (Munroe & Isaac, 2014). Croplands also harbour usefull trees that can function in agroforestry systems, which enhances food production and farmers' economic conditions in a sustainable manner (Dawson et al., 2013; Neupane & Thapa, 2001). The diversification of production is economically more sound than dependance on a single crop and protects soils from nutrient leaching, erosion, and over-drying (Barrett et al., 2013).

Emergent functional tree species group delineation resulted in an exotic trees species group and two groups dominated by indigenous species, although tree species origin (i.e. indigenous or exotic; cloud forest species or not) was not included in the analysis. This emphasises that the indigenous tree species have distinct tree traits and potential ecosystem services than exotic species. Three ecosystem services were also clearly attributed to exotic species (see above), while there were no ecosystem services that were strongly associated with indigenous species. Indigenous species deliver multiple services, like the provisioning of timber wood (e.g. termite resistant and durable construction wood of *Bridelia micrantha*), woodcraft (e.g. wood of *Maesa lanceolata* is used for making spoons and combs), forage (e.g. leaves of *Celtis africana* serve as fodder and relief them of indigestion), medicines (e.g. root extracts of *Clutia abyssinica* show antifungal and antiviral activities), etc. (Thijs, 2014). The local farmers have access to indigenous knowledge about tree resources and benefits (Barrett et al., 2013; Burkhard et al., 2012), which is also observed in other parts of Kenya or the world (Harvey et al., 2011; Kehlenbeck, Kindt, Sinclair, Simons, & Jamnadass, 2011). Our results show, however, that farmers can obtain the same ecosystem services from exotic species, and indeed, both exotic and indigenous tree species are used because their availability and well-known applications (Dodet & Collet, 2012). Therefore, the matrix does not only preserve a subset of the indigenous biodiversity but become a place for domestication and preservation of useful species (Ellis et al., 2012; Honnay, Jacquemyn, & Aerts, 2012; Perfecto & Vandermeer, 2008). Especially these landscapes with traditional farming systems play a crucial role in conserving such biodiversity, because there is a strong role for farmers in circa situm conservation (i.e. conservation of components of biological diversity by local farmers outside their natural habitats but within managed and traditional systems) (Dawson et al., 2013; Khumalo, Chirwa, Moyo, & Syampungani, 2012). The promotion of small-scale sustainable agriculture, as an integral component of tropical landscapes, is likely to preserve biodiversity in the long term. The small-scale agriculturalists more likely adopt sustainable agricultural technologies because they use few or no external inputs, use locally and naturally available materials, and generate agroecosystems that are more diverse and resistant to stress than capital intensive technologies (Perfecto & Vandermeer, 2010). But future changes in key social and ecological drivers are expected and ecosystem service trade-offs will arise, which can change type, magnitude, and relative mix of services provided by ecosystems (Maeda, Clark, Pellikka, & Siljander, 2010; Rodriguez et al., 2006). For instance, the loss of local knowledge on the ecosystem services delivered by indigenous plant species can result in a replacement of indigenous species by exotics.

More than 21% of the observed species in the matrix belonged to the cloud forest species group, which has group members that are typical for the Afromontane cloud forests. This group occurred significantly more in wooded sites and homesteads, than in croplands. The higher canopy cover of indigenous and exotic trees, probably facilitates the occurrence of the cloud forest species, for instance by providing shade. We refer to previous research in the study area, were cloud forest species were found in the smallest forest relicts and exotic tree plantations (Thijs et al., 2014a,b). Cloud forest species or indigenous species in general, cannot be protected in the matrix alone. Many of these species were not observed in the matrix and are completely restricted to remaining larger forest relicts (e.g. many endemic and late-successional species) (DeClerck et al., 2010; Gibson et al., 2011; Thijs et al., 2014a). The matrix is inhospitable for these species and the protection of the indigenous forest relicts is crucial for these species, but it is controversial in a region where poverty alleviation remains a more immediate priority than conservation (Gardner et al., 2010; Perfecto & Vandermeer, 2010; Tabarelli, 2010).

In this study, we linked 31 tree traits and ecosystem services to the landscape composition, but many more traits and services exist. The inclusion of such additional data will definitely result in further insights. For instance, certain trees or specific species are considered sacred (Burgess et al., 2007). They have different ways of affecting the society ranging from environmental services to protective and spiritual functions. These cultural trees are often old, indigenous species, which are strictly protected and therefore still present in the matrix. Further insights can be obtainted by the differentiation of planted and remnant trees (i.e. species persisting in the matrix originally occupied by forest or species that have (re)colonised remote areas, abandoned agricultural land or exotic tree plantations and inaccessible places), which are both a common feature in many human-modified forest landscapes worldwide (Herrera & Garcia, 2009; Manning et al., 2006). It is often difficult to determine the life history of a specific tree, but the inclusion of such information would certainly facilitate to find more distinctive patterns.

5. Conclusion

In this study, the role of trees in a human-modified landscape as provider of ecosystem services and their importance for biodiversity conservation has been addressed. A non-random distribution of tree traits occurred in the studied landscape. Croplands, characterised by low cover of indigenous forest and the lowest proportion of land used as fallow land or forest plantation, was dominated by individuals of the exotic tree species group. This group was characterised by large seeds and fruits, which corresponds with the many fruit tree in this group. Products of these trees have a high economic value, for instance by timber of the several plantation tree species. Other functional traits of the exotic tree species group is the nitrogen fixation and agroforestry potential. Two other emergent tree functional groups (i.e. cloud forest tree species group and small-leaved indigenous tree species group) were less common on croplands, but were significantly more abundant on wooded sites and homesteads. No functional traits were typical for these two species groups, which imply that these indigenous tree species are replaceable by exotics. Other indigenous species, including endemic or late-successional species were rare or absent in the matrix and their conservation can only be guaranteed by protecting the remaining indigenous forest fragments.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2015.07.015.

References

Aben, J., Adriaensen, F., Thijs, K. W., Pellikka, P., Siljander, M., Lens, L., et al. (2012). Effects of matrix composition and configuration on forest bird movements in a fragmented Afromontane biodiversity hot spot. *Animal Conservation*, *15*(6), 658–668. http://dx.doi.org/10.1111/j.1469-1795.2012.00562.x

Adriaensen, F., Githiru, M., Matthysen, E., & Lens, L. (2006). Modelling forest connectivity for critically-endangered bird species: A case study in the Taita Hills, Kenya. *Journal of Ornithology*, *147*(1), 125.

Aerts, R., November, E., Van Der Borght, I., Behailu, M., Hermy, M., & Muys, B. (2006). Effects of pioneer shrubs on the recruitment of the fleshy-fruited tree *Olea europaea* ssp cuspidata in Afromontane savanna. *Applied Vegetation Science*, *9*(1), 117–126. http://dx.doi.org/10.1658/1402-2001(2006)9[117:eopsot]2.0.co;2

Aerts, R., Thijs, K. W., Lehouck, V., Beentje, H., Bytebier, B., & Matthysen, E. (2011). Woody plant communities of isolated Afromontane cloud forests in Taita Hills, Kenya. *Plant Ecology*, *212*(4), 639–649. http://dx.doi.org/10.1007/s11258-010-9853-3

Barrett, K., Valentim, J., & Turner, B. L., II. (2013). Ecosystem services from converted land: the importance of tree cover in Amazonian pastures. *Urban Ecosystems*, *16*(3), 573–591. http://dx.doi.org/10.1007/s11252-012-0280-1

Beentje, H. J., & Ddiang'ui, N. (1988). An ecological and floristic study of the forests of the Taita Hills, Kenya. *Utafiti*, *1*(2), 23–66.

Burel, F., Lavigne, C., Marshall, E. J. P., Moonen, A. C., Ouin, A., & Poggio, S. L. (2013). Landscape ecology and biodiversity in agricultural landscapes. *Agriculture, Ecosystems & Environment*, *166*, 1–2. http://dx.doi.org/10.1016/j.agee.2013.01.001

Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Doggart, N. H., Fjeldsa, J., Howell, K. M., et al. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, *134*(2), 209–231. http://dx.doi.org/10.1016/j.biocon.2006.08.015

Burkhard, B., Kroll, F., Nedkov, S., & Muller, F. (2012). Mapping ecosystem service supply, demand and budgets. *Ecological Indicators*, *21*, 17–29. http://dx.doi.org/10.1016/j.ecolind.2011.06.019

Carreño-Rocabado, G., Peña-Claros, M., Bongers, F., Alarcón, A., Licona, J. C., & Poorter, L. (2012). Effects of disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology*, *100*(6), 1453–1463. http://dx.doi.org/10.1111/j.1365-2745.2012.02015.x

Chase, M. W., Thijs, K. W., Kamau, P., & Fay, M. F. (2013). *Dorstenia christenhuszii* (Moraceae), a new species from the Taita Hills, Kenya. *Phytotaxa*, *81*(2), 45–48. http://dx.doi.org/10.11646/phytotaxa.81.2.1

Dawson, I. K., Guariguata, M. R., Loo, J., Weber, J. C., Lengkeek, A., Bush, D., et al. (2013). What is the relevance of smallholders' agroforestry systems for conserving tropical tree species and genetic diversity in circa situm, in situ and ex situ settings? A review. *Biodiversity and Conservation*, *22*(2), 301–324. http://dx.doi.org/10.1007/s10531-012-0429-5

DeClerck, F. A. J., Chazdon, R., Holl, K. D., Milder, J. C., Finegan, B., Martinez-Salinas, A., et al. (2010). Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. *Biological Conservation*, *143*(10), 2301–2313. http://dx.doi.org/10.1016/j.biocon.2010.03.026

Di Gregorio, A. (2005). *Land cover classification system (LCCS), version 2: classification concepts and user manual. FAO environmental and natural resources series 8* Rome: FAO.

Dodet, M., & Collet, C. (2012). When should exotic forest plantation tree species be considered as an invasive threat and how should we treat them? *Biological Invasions*, *14*(9), 1765–1778. http://dx.doi.org/10.1007/s10530-012-0202-4

Dorrough, J., & Scroggie, M. P. (2008). Plant responses to agricultural intensification. *Journal of Applied Ecology*, *45*(4), 1274–1283. http://dx.doi.org/10.1111/j.1365-2664.2008.01501.x

Douglas, D. J. T., Nalwanga, D., Katebaka, R., Atkinson, P. W., Pomeroy, D. E., Nkuutu, D., et al. (2013). The importance of native trees for forest bird conservation in tropical farmland. *Animal Conservation*, *17*(3), 256–264. http://dx.doi.org/10.1111/acv.12087

Ellis, E. C., Antill, E. C., & Kreft, H. (2012). All is not loss: Plant biodiversity in the anthropocene. *PLos ONE*, *7*(1), 9. http://dx.doi.org/10.1371/journal.pone.0030535

Engeman, R. M., Sugihara, R. T., Pank, L. F., & Dusenberry, W. E. (1994). A comparison of plotless density estimators using Monte-Carlo simulation. *Ecology*, *75*(6), 1769–1779. http://dx.doi.org/10.2307/1939636

Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., et al. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, *12*(1), 22–33. http://dx.doi.org/10.1111/j.1461-0248.2008.01255.x

Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., et al. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*(6), 561–582. http://dx.doi.org/10.1111/j.1461-0248.2009.01294.x

Gardner, T. A., Barlow, J., Sodhi, N. S., & Peres, C. A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation*, *143*(10), 2293–2300. http://dx.doi.org/10.1016/j.biocon.2010.05.017

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., et al. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*(7369), 378–383. http://dx.doi.org/10.1038/nature10425

Girão, L. C., Lopes, A. V., Tabarelli, M., & Bruna, E. M. (2007). Changes in tree reproductive traits reduce functional diversity in a fragmented atlantic forest landscape. *PLos ONE*, *2*(9), 12. http://dx.doi.org/10.1371/journal.pone.0000908

Githiru, M., Lens, L., Adriaensen, F., Mwang'ombe, J., & Matthysen, E. (2011). Using science to guide conservation: From landscape modelling to increased connectivity in the Taita Hills, SE Kenya. *Journal for Nature Conservation*, *19*(5), 263–268. http://dx.doi.org/10.1016/j.jnc.2011.03.002

Harvey, C. A., Villanueva, C., Esquivel, H., Gomez, R., Ibrahim, M., Lopez, M., et al. (2011). Conservation value of dispersed tree cover threatened by pasture management. *Forest Ecology and Management*, *261*(10), 1664–1674. http://dx.doi.org/10.1016/j.foreco.2010.11.004

Herrera, J. M., & Garcia, D. (2009). The role of remnant trees in seed dispersal through the matrix: Being alone is not always so sad. *Biological Conservation*, *142*(1), 149–158. http://dx.doi.org/10.1016/j.biocon.2008.10.008

Herrera, J. M., & Garcia, D. (2010). Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. *Conservation Biology*, *24*(4), 1089–1098. http://dx.doi.org/10.1111/j.1523-1739.2010.01459.x

Hildebrandt, J. (1877). Von Mombassa nach Kitui. *Zeitschrift der Gesellschaft für Erdkunde*, *14*, 321–350.

Hilderbrand, R. H., Watts, A. C., & Randle, A. M. (2005). The myths of restoration ecology. *Ecology and Society*, *10*(1), 11.

Honnay, O., Jacquemyn, H., & Aerts, R. (2012). Crop wild relatives: More common ground for breeders and ecologists. *Frontiers in Ecology and the Environment*, *10*(3), 121. http://dx.doi.org/10.1890/12.wb.007

IBM. (2011). *IBM SPSS statistics for windows, Version 20.0*. Armonk, NY: IBM Corp.

Jesus, F. M., Pivello, V. R., Meirelles, S. T., Franco, G., & Metzger, J. P. (2012). The importance of landscape structure for seed dispersal in rain forest fragments. *Journal of Vegetation Science*, *23*(6), 1126–1136. http://dx.doi.org/10.1111/j.1654-1103.2012.01418.x

Katovai, E., Burley, A. L., & Mayfield, M. M. (2012). Understory plant species and functional diversity in the degraded wet tropical forests of Kolombangara Island, Solomon Islands. *Biological Conservation*, *145*(1), 214–224. http://dx.doi.org/10.1016/j.biocon.2011.11.008

Kehlenbeck, K., Kindt, R., Sinclair, F. L., Simons, A. J., & Jamnadass, R. (2011). Exotic tree species displace indigenous ones on farms at intermediate altitudes around Mount Kenya. *Agroforestry Systems*, *83*(2), 133–147. http://dx.doi.org/10.1007/s10457-011-9413-4

Khumalo, S., Chirwa, P. W., Moyo, B. H., & Syampungani, S. (2012). The status of agrobiodiversity management and conservation in major agroecosystems of Southern Africa. *Agriculture, Ecosystems & Environment*, *157*(0), 17–23. http://dx.doi.org/10.1016/j.agee.2012.01.028

Leakey, R. R. B. (2014). The role of trees in agroecology and sustainable agriculture in the tropics. *Annual Review of Phytopathology*, *52*, 113–133. http://dx.doi.org/10.1146/annurev-phyto-102313-045838

Lens, L., Van Dongen, S., Norris, K., Githiru, M., & Matthysen, E. (2002). Avian persistence in fragmented rainforest. *Science*, *298*(5596), 1236–1238, 10.1126%2fscience.1075664.

Maeda, E. E., Clark, B. J. F., Pellikka, P., & Siljander, M. (2010). Modelling agricultural expansion in Kenya's Eastern Arc Mountains biodiversity hotspot. *Agricultural Systems*, *103*(9), 609–620. http://dx.doi.org/10.1016/j.agsy.2010.07.004

Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures—Implications for conservation. *Biological Conservation*, *132*(3), 311–321. http://dx.doi.org/10.1016/j.biocon.2006.04.023

Mayfield, M. M., Ackerly, D., & Daily, G. C. (2006). The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology*, *94*(3), 522–536. http://dx.doi.org/10.1111/j.1365-2745.2006.01108x

McCune, B., & Mefford, M. (2002). *Analysis of ecological communities*. Gleneden Beach, OR: MjM Sofware Design.

Mendenhall, C. D., Karp, D. S., Meyer, C. F. J., Hadly, E. A., & Daily, G. C. (2014). Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, *509*(7499), 213–217. http://dx.doi.org/10.1038/nature13139

Metzger, J. P. (2000). Tree functional group richness and landscape structure in a Brazilian tropical fragmented landscape. *Ecological Applications*, *10*(4), 1147–1161. http://dx.doi.org/10.2307/2641023

Moran, C., Catterall, C. P., & Kanowski, J. (2009). Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation*, *142*(3), 541–552. http://dx.doi.org/10.1016/j.biocon.2008.11.006

Munroe, J. W., & Isaac, M. E. (2014). N-2-fixing trees and the transfer of fixed-N for sustainable agroforestry: A review. *Agronomy for Sustainable Development*, *34*(2), 417–427. http://dx.doi.org/10.1007/s13593-013-0190-5

Neupane, R. P., & Thapa, G. B. (2001). Impact of agroforestry intervention on soil fertility and farm income under the subsistence farming system of the middle hills, Nepal. *Agriculture, Ecosystems & Environment*, *84*(2), 157–167. http://dx.doi.org/10.1016/s0167-8809(00)00203-6

Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B., et al. (2010). Biodiversity in a forest-agriculture mosaic—The changing face of West African rainforests. *Biological Conservation*, *143*(10), 2341–2350. http://dx.doi.org/10.1016/j.biocon.2009.12.032

Pellikka, P., Clark, J. F., Gosa, A. G., Himberg, N., Hurskainen, P., Maeda, E., et al. (2013). Agricultural expansion and its consequenses in the Taita Hills, Kenya. In P. Paron, D. Olago, & C. T. Omuto (Eds.), *Kenya: A natural outlook* (pp. 165–179). Amsterdam: Elsevier.

Pellikka, P. K. E., Lotjonen, M., Sijander, M., & Lens, L. (2009). Airborne remote sensing of spatiotemporal change (1955–2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. *International Journal of Applied Earth Observation and Geoinformation*, *11*(4), 221–232. http://dx.doi.org/10.1016/j.jag.2009.02.002

Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems—A new conservation paradigm. *Annals of the New York Academy of Sciences*, *1134*, 173–200. http://dx.doi.org/10.1196/annals.1439.011

Perfecto, I., & Vandermeer, J. (2010). The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(13), 5786–5791. http://dx.doi.org/10.1073/pnas.0905455107

Rodriguez, J. P., Beard, T. D., Bennett, E. M., Cumming, G. S., Cork, S. J., Agard, J., et al. (2006). Trade-offs across space, time, and ecosystem services. *Ecology and Society*, *11*(1), 28, 14.

Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W. W., et al. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, *5*(2), 107–121. http://dx.doi.org/10.1078/1439-1791-00216

Schmidt, P. (1989). Early exploitation and settlement in the Usambara Mountains. In A. C. Hamilton, & R. Bensted-Smith (Eds.), *Forest conservation in the East Usambara Mountains Tanzania* (pp. 75–79). Gland: IUCN Tropical Forest Programma.

Tabarelli, M. (2010). Tropical biodiversity in human-modified landscapes: What is our trump card? *Biotropica*, *42*(5), 553–554. http://dx.doi.org/10.1111/j.1744-7429.2010.00678.x

Thijs, K. W. (2014). Field guide to the woody plant species of Taita Hills, Kenya. *Journal of East African Natural History*, *102*(1&2), 1–283. http://dx.doi.org/10.2982/028.102.0101

Thijs, K. W., Aerts, R., Musila, W., Siljander, M., Matthysen, E., Lens, L., et al. (2014). Potential tree species extinction, colonization and recruitment in Afromontane forest relicts. *Basic and Applied Ecology*, *15*(4), 288–296. http://dx.doi.org/10.1016/j.baae.2014.05.004

Thijs, K. W., Aerts, R., Van de Moortele, P., Musila, W., Gulinck, H., & Muys, B. (2014). Contrasting cloud forest restoration potential between plantations of different exotic tree species. *Restoration Ecology*, *22*(4), 472–479. http://dx.doi.org/10.1111/rec.12093