

Drivers of topsoil saturated hydraulic conductivity in three contrasting landscapes in Kenya

Restoring soil hydraulic conductivity in degraded tropical landscapes

Huvudfaktorer bakom infiltrationskapacitet i tre kontrasterande landskap i Kenya

David Falk

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David Falk

Supervisor:	Aida Bargués Tobella, SLU, Department of Forest Ecology and Management
Deputy supervisor:	Ulrik Ilstedt, SLU, Department of Forest Ecology and Management
Deputy supervisor:	Leigh Winowiecki, ICRAF
Deputy supervisor:	Tor-Gunnar Vågen, ICRAF
Deputy supervisor:	Madelon Lohbeck, Wageningen University, Forest Ecology and Forest Management
Examinator:	Gert Nyberg, SLU, Department of Forest Ecology and Management

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Swedish University of Agricultural Sciences Faculty of Forest Sciences

Department of Forest Ecology and Management

Sammanfattning

Markförsämring i tropiska regioner kan ha förödande konsekvenser för vattentillgänglighet. Vattenkvalité och kvantitet är oerhört viktiga för lokalbefolkningar och är grundförutsättningar för socioekonomisk utveckling då stora delar av befolkningen i många tropiska länder är direkt beroende av jordbruk och boskapshållning för sin inkomst. En strategi för att öka mängden tillgängligt vatten i torra tropiska ekosystem är att öka hastigheten och kvantiteten av vattennederbörd som infiltreras i jorden. Olika faktorer samspelar i infiltrationskapaciteten, däribland vegetation, jordart och markanvändning. Förståelsen för hur olika variabler påverkar markens hydrologiska funktioner på landskapsnivå är begränsad. Det behövs mer forskning kring hur biologisk mångfald och vegetationsmängd påverkar infiltration. En vetenskaplig förståelse för hur dessa variabler påverkar infiltrationskapacitet är avgörande för effektiviteten av restaureringsinitiativ i tropiska områden som har försämrade vattentillgångar. Syftet med detta examensarbete är att undersöka huvudfaktorerna som påverkar infiltrationskapacitet i tre kontrasterande lokaler i Kenya, för att förstå vad som driver infiltration på en övergripande landskapsnivå.

Linjära mixade modeller användes för att urskilja de viktigaste variablerna både i, och mellan de tre lokalerna. Variabler relaterade till markegenskaper, vegetationsmängd, funktionell biodiversitet, markanvändning och markförsämring inkluderades i modellerna. Resultaten visade att de statistiskt viktigaste variablerna var jordart, markanvändning, erosion och funktionell biodiversitet, för den modell som beskrev alla tre lokaler. Tre ytterligare modeller konstruerades och kunde påvisa att resultaten på enskild lokalnivå var annorlunda, då infiltrationskapaciteten i grovkornig jord var mest påverkad av jordart. I finkornig jord var andra variabler viktigare, så som markanvändning och markförsämring. Infiltrationskapaciteten är naturligt högre i grovkornig jord, därför har restaureringsinitiativ minimal effekt. Finkornig jord har lägre infiltrationskapacitet som i högre utsträckning skulle kunna påverkas av anpassad restaurering inriktad på att öka befintlig vegetation och minimera markanvändning som leder till markförsämring. Den här studien visar att olikheter i infiltrationskapacitet är relaterade till markegenskaper, vilket understryker behovet av restaureringsinitiativ som är anpassade till lokala förhållanden.

Nyckelord: Infiltrationskapacitet, linjär mixad modell, Kenya, markförsämring, funktionell diversitet, vegetation

Abstract

Land degradation in the tropics has severe impacts on the availability of water and can lead to decreased rates of infiltration. Reduced infiltrability leads to less water availability, which negatively impacts livelihoods and hinders socioeconomic development. Understanding the drivers of infiltrability is essential for managing landscapes in the tropics, particularly when implementing restoration measures to improve soil hydrological function. The aim of this thesis is to identify the factors driving infiltrability across three different landscapes in Kenya.

Linear mixed effects models were conducted to identify the main factors affecting infiltrability across and within sites, based on data from the Land Degradation Surveillance Framework. Variables related to inherent soil properties, land use, land degradation, functional diversity and vegetation cover were included in the model. Results indicate that the main factors increasing infiltrability across the three sites are land use, functional evenness and soil texture, while erosion decreases infiltrability. In coarse-grained soils, texture is the dominating factor while in fine-grained soils land use and degradation are more important. Hence, as infiltrability is inherently high in coarse-grained soils, improving soil hydrological function is not necessary. On the contrary, fine-grained soils have lower infiltrability that can be improved by adaptive restoration measures that target increasing continuous vegetation cover and minimizing land use practices that lead to land degradation. Therefore, this study demonstrates that differences in infiltrability are related to inherent soil properties, which emphasize the need for restoration measures adapted to an understanding of local site conditions.

Keywords: Infiltrability, mixed effects model, Kenya, land degradation, functional diversity, vegetation

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Abbreviations

CWM	Community-Weighted Mean				
FAO	Food and Agriculture Organization				
FD	Functional Diversity				
FEve	Functional Evenness				
FDis	Functional Dispersion				
FDiv	Functional Divergence				
FRic	Functional Richness				
ICRAF	World Agroforestry				
K_{fs}	Field-saturated hydraulic conductivity				
K _{fs} K _s	Field-saturated hydraulic conductivity Saturated hydraulic conductivity				
10					
K _s	Saturated hydraulic conductivity				
K _s LCCS	Saturated hydraulic conductivity Land Cover Classification System				
K _s LCCS LDSF	Saturated hydraulic conductivity Land Cover Classification System Land Degradation Surveillance Framework				

1. Introduction

Billions of people worldwide suffer from inadequate access to freshwater and an increasing demand has resulted in freshwater scarcity becoming one of the main obstacles to sustainable development (Mekonnen & Hoekstra 2016; Ellison et al. 2017). Land degradation in the tropics negatively affects both water quality and water quantity for local populations (Bossio et al. 2010). Land degradation is a complex issue involving societal and biophysical factors (Mganga et al. 2015; Vågen et al. 2016; Kimiti et al. 2017) such as drought, deforestation and following conversion to agricultural land, poor land management practices, and excessive grazing (Lal 1996; Gisladottir & Stocking 2005; Zimmerman & Elsenbeer 2008; Vasu et al. 2018). Land degradation can be aggravated by both drought and climate change (Webb et al. 2017) and may manifest as increased erosion, crust formation, less organic carbon in soils and reduced infiltrability (Bruijnezeel 2004; Nyberg et al. 2012). This, in turn, can lead to decreased water quality and quantity as well as changes in timing of water supply which negatively impacts water security. Water availability is instrumental for socioeconomic development (United Nations 1997) and its scarcity limits growth of livelihoods (Falkenmark et al. 1989). Therefore, when faced with the exacerbating effect of both natural and human impact on land degradation, ensuring adequate hydrological function in soils is crucial for safeguarding human livelihoods.

Management of freshwater in the seasonally dry tropics is challenging due to the variable nature of rainfall both in time and space and prevalent high rainfall intensities (Wohl et al. 2012). In tropical drylands, the characteristics of rainfall high rainfall intensity, few rainfall events and a high spatiotemporal heterogeneity - limits production and challenges food security (Falkenmark 1989; Rockström et al. 2010). Precipitation patterns in the tropics are expected to vary in the future due to climate change, with projections indicating a reduction in total precipitation (Ringler et al. 2010) and an increase in the frequency of highintensity rainfall events (Seneveratne et al. 2012). The challenge of water management is further compounded in degraded soils, where heavy rain can trigger increased surface runoff and erosion, which exposes subsoils that have even lower infiltrability and water absorption capacity (Eckholm 1976). Improving soil hydrological function is thus key to increase water and food security (Malmer et al. 2010). In particular, the improvement of soil infiltration is fundamental. It can lead to less surface runoff and more water percolating into soils, thereby increasing the recharge of soil water and eventually that of groundwater, and the time needed for water to reach streams (Hillel 1971; Bonell 1993; Ilstedt et al. 2007; García-Gutiérrez et al. 2017). Soil infiltrability, also known as infiltration capacity, is defined as: "the flux which the soil profile can absorb through its surface when it is maintained in contact with water at atmospheric pressure" (Hillel 1971).

When water is applied and maintained at the surface of initially dry soils, soil infiltrability is generally high and tends to gradually decrease with time until asymptotically approaching a constant rate at saturation. This rate is known as the steady-state infiltrability or final infiltration capacity (Hillel 1971). During initial stages of infiltration in unsaturated soils, water is transported downwards through suction and gravity gradients. The influence of the suction gradient progressively decreases as the soil profile becomes wetter due to factors such as swelling of clay, air bubbles becoming trapped in the soil profile and surface crust formation (Hillel 1971). This leads to the infiltration rate settling at a near constant controlled by gravity. As gravity becomes the dominant factor for infiltration of water, the hydraulic conductivity of the soil becomes the controlling factor for the flux of water. Therefore, we assume that the steady-state infiltrability is equivalent to the saturated hydraulic conductivity (K_s), which is the hydraulic conductivity of soils when the soil matrix is saturated. Field-saturated hydraulic conductivity (K_{fs}) is the measurement of K_s in field conditions, and tends to be lower than conductivity measured in entirely saturated states achievable under artificial conditions (Nimmo et al. 2009). K_{fs} depends largely on soil's particle size distribution, with coarse-textured soils containing larger pore sizes typically having a greater K_{fs} compared to more fine-textured soils (Blackburn 1975; Hillel 1980; van Schaik et al. 2009; García-Gutiérrez et al. 2017). However, it is also influenced by soil structure, which is affected by management. Hence, there is scope for implementing restoration measures that target infiltrability and overall hydrological function of tropical soils.

Using trees in restoration strategies in tropical regions can be an effective way of improving hydrological function. Trees can have a positive effect on infiltrability and preferential flow through creating macropores in soils via root structures, improving soil structure and aggregation through above- and belowground litter inputs, and through increasing soil macrofauna (Mando et al. 1996; Léonard et al. 2004; Ilstedt et al. 2007; van Schaik 2009; van Schaik et al. 2014; Kuhyah et al. 2016; Bargués-Tobella et al. 2014; Bargués-Tobella et al. 2019). Preferential flow is the non-uniform vertical movement of water in soils along specific pathways that bypass the porous matrix, such as cracks, earthworm burrows and tree root channels (Hendrickx & Flury 2001). More soil organic

matter prevents soil crust formation by reducing the breakdown and dispersion of aggregates when the soil surface is exposed to rainfall (Lado et al. 2004). Increased infiltrability and preferential flow in the proximity of trees can also lead to improved groundwater recharge (Ilstedt et al. 2016) and results from Bargués-Tobella et al. (2014) showed that preferential flow increased in areas with higher tree density. In addition, the clustered growth of trees in savannah landscapes creates fertility islands with elevated levels of soil organic matter content (Schlesinger et al. 1990; Ridolfi et al. 2008). Despite the documented benefits of trees, there is a lack of scientific understanding concerning the role of specific tree species on soil hydrological function (Ilstedt et al. 2007; Malmer et al. 2010; Sanou et al. 2010). Due to this research gap it remains unclear if certain species or specific functional traits improve infiltrability. A functional trait is a measurable property of an organism that has a large influence on its performance and can be used comparatively across different species (McGill et al. 2006). Therefore, despite the repeatedly documented positive impacts of trees on infiltrability, questions still remain concerning the effect of both quantity and quality of vegetation on improving soil hydrological function.

Functional strategies of different tree species affect their environment and subsequently soil conditions in different ways. Research suggests that functional diversity and composition influences ecosystem function primarily through increased resource-use efficiency (Díaz & Cabido 2001; Botta-Dukát 2005; Cadotte et al. 2011; Zhu et al. 2015). Trees with conservative resource-use strategies tend to be more drought-resistant and invest more resources in wood and leaves, resulting in higher wood density and tougher leaves (Díaz et al. 2004; Markesteijn et al. 2011; Wigley et al. 2016). Species with an acquisitive strategy have deeper root systems, lower wood densities and often shed their leaves (deciduousness) in order to cope with drought (Taneda & Sperry 2008; Pineda-García et al. 2013; Bai et al. 2015). Furthermore, nitrogen fixation can lead to increased nutrient input from litter leading to greater primary productivity, which affects total carbon sequestration and aboveground biomass of trees (Resh et al. 2002; de Deyn et al. 2008; Tchichelle et al. 2017). Species-specific resource-use strategies will impact soil properties in different ways through adding organic matter input, altering macrofauna abundance and affecting decomposition rates (Pérez-Harguindeguy et al. 2000; Loranger-Merciris et al. 2007; de Deyn et al. 2008). By directly affecting soil properties, different functional traits will have an impact on soil hydraulic properties and water availability. Understanding the relationship between functional traits and soil properties would improve ecological restoration through allowing selection of the most suitable species in degraded land (Hao et al. 2020). As increased functional diversity can positively affect ecosystem functioning, this effect should include soil hydraulic properties. Higher functional diversity, leading to increased resource-use efficiency and greater productivity, may result in increased infiltrability.

Besides tree cover and inherent soil properties such as soil texture, there are several factors that can influence soil infiltrability. The pH of soils affects clay dispersion (Mills et al. 2006) and other soil properties like nitrogen and carbon content also influence infiltrability (Franzluebbers 2002; Mills et al. 2006). Dynamic variables dictated by land use can have an impact on infiltration rates, such as high grazing intensity (Weltz et al. 1989; Mwendera & Saleem 1997). Specific macrofauna have been found to positively affect infiltration capacity through increasing preferential flow via the creation macropores, such as earthworms (Fischer et al. 2015) and termites (De Deyn et al. 2008; Bargués Tobella et al. 2014). Variables related to vegetation such as the fine-root length of grasses have a stabilizing effect on soil physical structure that can positively influence infiltration (Hao et al. 2020). Although a variety of studies have shown positive links between vegetation and infiltrability, there are still contrasting results concerning different vegetation types and the interplay factors related to soil properties and vegetation (Hao et al. 2020). A holistic understanding of the infiltration process and how it is connected to soil properties, which in turn are affected by numerous other factors, is essential for effective soil and water management (Hillel 1971).

A full understanding of what factors affect infiltrability requires consideration of the driving roles of the aforementioned variables and how their influence varies on a landscape scale. The majority of studies concerning the effect of vegetation or land use changes on infiltrability are conducted on a limited spatial scale considering variables such as K_{fs} under tree canopy vs. open ground. For example, studies such as Fischer et al. (2015) and Liu et al. (2019) that describe a positive relationship between plant diversity and infiltrability have results that are highly localized. Consequently, soil conditions are often uniform which leads to conclusions being mostly relevant to local conditions. Research is lacking with regard to larger spatial scales with varying biophysical conditions such as soil properties, topography and climate.

There is a need to deepen the understanding of landscape-level drivers of infiltrability, in order to implement effective management strategies to restore and retain soil hydrological function. Evidently, multiple variables can have positive effects on infiltrability. Discerning which variables are the driving factors behind differing rates of infiltration will allow for conclusions to be drawn concerning what ecosystem characteristics are most important, with regards to hydrological function. The dataset used in this study will incorporate variables related to woody functional traits, soil health indicators, inherent soil properties including soil texture, vegetation patterns, land use and land degradation. The objective of this study is to assess what factors affect infiltrability the most across three

contrasting landscapes in Kenya with different soil properties and vegetation patterns. Coarser-textured soils and variables related to woody vegetation, such as vegetation quantity and functional diversity, are hypothesized to have a positive effect on K_{fs} . Measures of land degradation, such as grazing intensity and erosion, are expected to have a negative effect on K_{fs} . Through examining the effect of the aforementioned range of different variables across the three sites, drivers of K_{fs} can be identified on the landscape-level. The main drivers at the site-level will also be identified, in order to distinguish how different site conditions change which factors are dominant in driving K_{fs} .

2. Methodology

2.1. Site Description

Data was gathered from three 100km² sites in Kenya: Muminji, Thange and Kubo South (

Figure 1). All the sites contain different types of land uses and cropland, such as annual cropland with agroforestry and perennial cropland systems. A wide variety of crops are cultivated in the sites, including maize (*Zea mays* L.), cowpea (*Vigna unguicolata* L.), green grams (*Vigna radiata* L.), cashew (*Anacardium occidentale* L.) and khat (*Catha edulis* Vahl.). The majority of sampled plots were privately owned. The three sites have contrasting climates and represent a gradient in aridity (*Table 1*). Kubo South is located on the southern coast of the country, in Kwale County, and has the highest average annual precipitation of the sites. Thange is located in the south, in Makueni County, and is markedly drier than the other sites. Muminji is situated more centrally, in Embu County, and at the highest elevation.

Site	Aridity Class	Average Aridity Index	Köppe-Geiger Climatic Zone	Average Mean Annual Precipitation (mm)	Average Elevation (m)
Kubo South	Humid	0.8	Equatorial savannah with dry summer (As)	1255.6	90.5
Muminji	Dry sub- humid	0.5	Equatorial savannah with dry winter (Aw)	922.9	1117.5
Thange	Semi-arid	0.3	Equatorial savannah with dry winter (Aw)	609.8	919.5

Table 1. Average site descriptive data based on individual plot values (Kottek et al. 2006; Fick & Hijmans 2017; Trabucco & Zomer 2019).



Figure 1. Map of site locations. A) Muminji, B) Thange, C) Kubo South. Each yellow point represents a plot.

2.2. Soil and Land Health Survey

The sites were sampled following the Land Degradation Surveillance Framework (LDSF), as part of the Kenya Cereals Enhancement Programme - Climate Resilient Agricultural Livelihoods Window (KCEP-CRAL) project in 2018-2019. The LDSF was developed by World Agroforestry (ICRAF) in order to establish a biophysical baseline for monitoring landscape degradation and assessing the effectiveness of restoration measures in tropical landscapes (Vågen & Winowiecki 2020). The LDSF consists of a hierarchical field survey and sampling design with sites that are 100km² (10 x 10km) in size (*Figure 2*). Each site is divided into 16 tiles (2.5km x 2.5km). Within each tile centroid locations for clusters are randomized. Each cluster contains 10 plots, with randomized centrepoints pinned out within a 564m radius from the centroid of the cluster. Each individual plot is 1000m² and contains 4 subplots that are 100m² in size. Thus, the methodology results in a spatially stratified randomized sampling design that minimizes local biases. See *Appendix Table 1* for a complete list of variables and corresponding units.



Figure 2. LDSF field survey design. Consists of a 10×10 km site containing 16 clusters, each with ten $1000m^2$ plots. Each plot contains four $100m^2$ subplots.

Data concerning vegetation structure, land management and land-use history was collected at the plot-level (1000 m^2). Plots were classified using the Food and Agriculture Organization's (FAO) Land Cover Classification System (LCCS) based on the predominant vegetation structure into seven categories: bushland, grassland, cropland, woodland, thicket, wooded grassland and shrubland. The LCCS was created under the FAO AFRICOVER project (di Gregorio & Jansen 2000). Plots were also categorized based on the predominant land use and vegetation cover into seven classes: agroforestry with annual crops, annual cropland, fallow, other, agroforestry with perennial crops, perennial cropland, and rangeland. In this study, the rangeland class was further divided into two, in order to distinguish between closed rangeland with trees and open rangeland without trees. The vegetation of the plots was distinguished using the classification system in White (1983) (Table 2). Plots identified as rangeland and bushland, wooded grassland, woodland or thicket were categorized as closed rangeland, while plots identified as rangeland and grassland or shrubland were classified as open rangeland. The annual crop class was used for plots where crops such as maize, beans and green grams were cultivated, while the perennial crop class included fruit trees such as orange tree (*Citrus sinensis* L.), pigeon peas (*Cajanus cajan* L.) and cashew. Both classes were categorized as agroforestry when there was tree cover in the plot other than tree crops.

Туре	Description			
Bushland	A mix of trees and shrubs with a canopy cover of $\geq 40\%$.			
Cropland	Cultivated land with annual or perennial crops.			
Grassland	Land covered with grasses and other herbs. Woody vegetation may be absent or $<10\%$.			
Shrubland	Open or closed stand of shrubs ≤3m tall.			
Thicket	A closed stand of bushes and climbers 2 - 7m tall.			
Wooded Grassland	Land covered with grasses and other herbs, with a woody vegetation cover of 10 - 40%.			
Thicket	An open stand of trees with a canopy cover of ≥40%. Field layer usually dominated by grasses.			

Table 2. Description of classes for vegetation structure variable in LDSF dataset; based on White (1983).

At the subplot-level (100 m²), measurements were taken on erosion and vegetation cover. Erosion was recorded in each subplot based on signs of three different erosion types: sheet, rill and gully. Sheet erosion is the uniform removal of soil in thin layers and is more common in overgrazed and cultivated soils. Signs of sheet erosion are bare areas, visible tree roots and puddling of rainfall on the soil surface. Rill erosion is the next stage of soil erosion and manifests as shallow drainage lines <30cm deep (rills can be removed by tillage). Gully erosion is caused by water cutting through soil along flow pathways of runoff, creating gully channels >30cm deep. Gullies can not be removed by tillage. Plots were also assigned a binary classification of 0 or 1 based on the presence, or lack thereof, of the three erosion categories.

Impact on habitat variables, including grazing, agriculture and erosion, were surveyed on the plot-level through using a score of 0-3. The impact of the aforementioned variables on each individual subplot was surveyed qualitatively and reflects the intensity of impact of the variables on the habitat. If three or four subplots showed signs of an impact variable, for example grazing, the plot was assigned a score of 3. If there were no signs of the specific impact variable in any of the subplots, the plot received a score of 0.

Within each subplot, all woody plants - i.e. shrubs (1.5-3m height) and trees (>3m height) - were counted, measured and identified. Woody and herbaceous cover was measured in each subplot using the Braun-Blanquet vegetation rating scale (Braun-Blanquet 1928). The rating scale spans from 0 (bare ground) to 5 (>65% cover). Every tree and shrub was identified to at least the genus level. Tree height and circumference were recorded for each individual tree, and shrub height, width and length for all shrubs. Plot-level estimates for shrub, tree and

total woody cover as well as density were calculated through averaging the subplot values.

Soil samples were collected using an auger at the centre of each subplot at two depth intervals, 0-20cm (topsoil) and 20-50cm (subsoil). The subplot soil samples from each depth interval were pooled together resulting in two composite plot-level soil samples for each plot: one for topsoil and one for subsoil.

2.3. Soil Laboratory Analyses

Samples were initially air-dried and ground in order to pass through a 2mmsieve. A subset (10% of samples) of the total top- and subsoil samples were analysed for pH, exchangeable bases, texture and organic carbon using wet chemistry methods. Values for pH were derived through mixing 20g of soil with 40mL of de-ionized water. The solution was shaken for 30 minutes and subsequently remained stationary for 20 minutes before pH analysis on a Eutech Cyberscan 1100 meter. A solution of 3g of soil and 30 mL of Mehlich-3 extracting solution was used to obtain values for exchangeable bases after placing the filtrate on a reciprocating shaker and shaken for 5 minutes. Inorganic carbon was removed prior to measurement of nitrogen and organic carbon using 0.1 N HCl. The total nitrogen and organic carbon were measured using dry combustion with an Elemental Analyzer Isotope Ratio Mass Spectrometry (EA-IRMS) from Europa Scientific at the IsoAnalytical Laboratory in the United Kingdom. Sand content was measured in Nairobi at the ICRAF Soil-Plant Spectral Diagnostics Laboratory. Each soil sample was shaken for 4 minutes in a 1% sodium hexametaphosphate solution before being placed for analysis in a Laser Diffraction Particle Size Analyzer (LDPSA) from HORIBA (LA 950).

A selection of soil samples was also analyzed for mid-infrared (MIR) absorbance using the Tensor 27 HTS-XT from Bruker Optics at the ICRAF Soil–Plant Spectral Diagnostics Laboratory in Nairobi, Kenya. The MIR spectra was processed using the methodology described in Terhoeven-Urselmans et al. (2010).

Soil samples with both wet chemistry data and MIR spectra were used to develop random forest models to predict the different soil properties for the remaining soil samples (Vågen et al. 2016). This study used only results from topsoil samples and excluded subsoil samples from the dataset.

2.4. Soil Infiltrability

Soil infiltration was measured in 3 plots per cluster in Thange and Kubo South, while 5-6 were performed per cluster in Muminji. The measurements were

randomly assigned to plots within the cluster. Measurements were conducted in the centre of the plot. Infiltrability was measured using a single-ring infiltrometer (Bouwer 1986), as they are more time-efficient and allow for repeated measurements across different plots due to lower water use than double-ring infiltrometers. The distance from the infiltration measurement point to the nearest shrub and tree was recorded.

A single-ring infiltrometer with an inner diameter of 15.6 cm and 17cm high was placed in the centre of subplot 1 and carefully pushed at least 2 cm into the soil to minimize disturbance of the soil surface. The soil surface inside the infiltrometer was pre-wetted through slowly pouring water into the infiltrometer to avoid soil surface disturbance. After 15 minutes of pre-wetting, infiltrability measurements were initiated. An upright ruler was fixed to the inside of the infiltrometer. The ruler was used to fill the infiltrometer with water to the starting level (e.g. 16 cm) and to read the water level after a certain time interval. During the first 30 minutes of the infiltration experiment, the water level in the infiltrometer was recorded at 5-minute intervals. After recording the water level, the infiltrometer was immediately refilled to the initial starting level. The time interval was increased to 10 minutes during the subsequent 30 minutes, and was increased again to 20 minutes during the remaining infiltrability measurement period, which lasted 2.5 hours in total to ensure that steady-state conditions were attained. The formula from Nimmo et al. (2009) was used to derive K_{fs} from the field infiltration measurements. This formula corrects for hydrostatic pressure, falling-head and the effects of lateral spread of water.

2.5. Calculations

2.5.1. Functional Traits of Woody Species

The LDSF dataset was supplemented with data on functional traits. Four functional traits were used for the calculation of functional properties of woody vegetation: wood density, specific leaf area (SLA), deciduousness and nitrogen fixation. These traits were selected based on availability of public data and feasibility of sourcing information for tropical species. Data on these four functional traits was obtained using literature search for all 260 species of woody plants in the dataset.

Wood density (g cm⁻³), or wood specific gravity, was a necessary parameter for calculating aboveground biomass of trees and shrubs (see section 2.5.2). Wood density values were sourced from a variety of databases (*Appendix Table 2*). In order to eliminate outlier values, a median wood density was calculated when there were different density values for the species. When possible, wood density

values obtained from tree samples in Africa were used. In the absence of a species-specific wood density, a genus density was calculated through finding the median of all species-specific densities in the genus. When wood density values for a specific species or the genus it belongs to were not available, a median density based on family was calculated using the dataset from Zanne et al. (2009).

Values for SLA (mm² mg⁻¹) were obtained from the TRY Plant Trait Database (Kattge et al. 2020) (*Appendix Table 3*). Median SLA values specific to each species were used when possible. If species-specific information was not available, a median genus SLA value was derived. If the database contained no information on any species in the genus, a family-level median SLA was used. Due to inconsistent information concerning study site locations, all SLA values were based on global data.

The values for deciduousness were obtained principally based on local data, due to significant regional variation in classification of species leaf-shedding characteristics. Species were classified as evergreen (0), semi-deciduous (0.5) or deciduous (1) based on literature search (Maundu & Tengnäs 2005; Iversen et al. 2017; Kattge et al. 2020; Fern 2019) (*Appendix Table 4*). Values from global literature were used when local data was unavailable. When information was conflicting concerning a species' leaf-shedding characteristics, the most frequently occurring classification was used. Out of the 260 woody species included in the dataset, 249 were categorized while sparse or lack of information made classification of the remaining 11 unreliable. For individual trees and shrubs identified exclusively at the genus level, a mode of deciduousness values was used for species in the genus.

Species' capacity for nitrogen fixation was given a binary score (1 or 0) based on their ability to fix nitrogen or not (*Appendix Table 5*). Local data was used, if available, when scoring species. Species belonging to the *Leguminosae* family were assumed to be nitrogen-fixing when no literature data was available. This assumption was based on 88% of species in the family forming a symbiotic relationship with nitrogen-fixing microbes in the root systems (de Faria et al. 1989). Species not part of the *Leguminosae* family were assumed to be non nitrogen-fixing when no literature sources specifically stated that they were.

2.5.2. Aboveground Woody Biomass

The LDSF dataset was supplemented with calculations for woody biomass. Subplot-level aboveground biomass was calculated for trees and shrubs based on multiple allometric equations. The subplot biomass was summed in order to get the plot-level biomass. Equations from Chave et al. (2005) and Chave et al. (2014) were used to calculate aboveground biomass for all trees except for Adansonia digitata L. Chave et al. (2005) provide allometric equations for different forest types. The equation for dry forest stands was used, as the mean annual precipitation was less than 1500 mm year⁻¹ at all sites. Chave et al. (2014) presents a singular best-fit pan-tropical allometric equation. The equations used from the two studies were both based on diameter at breast height (cm), height (m) and wood specific gravity (g cm⁻³). The average value between the aboveground tree biomass estimates obtained with the two equations was calculated to produce a final value. The formula in Conti et al. (2013) was used to estimate aboveground biomass for shrubs based on height (cm), crown area (cm²) and wood specific gravity (g cm⁻³).

A separate allometric equation from Malimbwi et al. (2016) was applied to estimate the aboveground biomass of *Adansonia digitata* L. trees. The pantropical allometric equations for the other species in the dataset were not suitable due to the unique nature of these trees, which have low wood density and are often hollow. Hence, a species-specific equation was applied for biomass estimations of *A. digitata*. As recommended by Malimbwi et al. (2016), the measurement input for the allometric equation was exclusively DBH, as the rounded crowns of the species complicates height measurements. Wood specific density values were obtained as described in section 2.5.1. For five tree species a site-averaged value for wood-specific gravity was used (Chave et al. 2005), as the species were identified only using their local names. The same was done for seven shrub species.

2.5.3. Functional Properties of Woody Vegetation

The LDSF dataset was supplemented with data on functional diversity (FD). FD indices and community-weighted means (CWM) of woody vegetation were calculated at the plot-level using the FD package in R (Laliberté et al. 2014) based on the four functional traits included in this study: wood density, SLA, deciduousness and nitrogen-fixation. The functional diversity indices were computed based on the total species abundance (number of individuals of each species present in the plot) and the total biomass (aboveground biomass of each species in the plot).

The following indices were calculated and included in the modelling analysis: functional richness (FRic) (Villéger et al. 2008), functional evenness (FEve) (Villéger et al. 2008), functional divergence (FDiv) (Mason et al. 2005), functional dispersion (FDis) (Laliberté & Legendre 2010) and Rao's Quadratic Entropy (RaoQ) (Botta-Dukát 2005). Additionally, the CWMs for all four traits were also calculated. FRic is not affected by the abundance of species, is strongly related to the quantity of different species and signifies the amount of functional

space that species occupy (Villéger et al. 2008). FEve represents the evenness in species abundance distribution within the functional trait space of a community, and reflects the under- or overutilization of resources (Mason et al. 2005). FEve also describes if the functional traits are distributed regularly in the functional trait space based on species abundances. FDiv describes niche differentiation by measuring how species abundance is partitioned on the functional trait axis of a community (Mason et al. 2005). FDis describes the mean distance of individual species to the centroid of the total functional traits in a community (Laliberté & Legendre 2010). Lastly, like FDis, RaoQ also measures how species are distributed in the functional trait space but as opposed to comparing species based on the centroid it measures the mean distance between two randomly selected species in a community (Botta-Dukát 2005; Laliberté & Legendre 2010).

All measures of FD were included in the statistical analysis in order to elucidate which aspect of functional diversity has the greatest effect on ecosystem function. In addition, functional diversity cannot be calculated in plots with less than 3 functionally singular species. For these plots all FD indices and CWM values were identified as 0, in order to indicate no functional diversity.

2.6. Statistical Analysis

The original dataset was scaled down in order to make modelling feasible. Plots where infiltrability was not measured were removed. Additionally, four plots were removed from the Thange dataset, as they were considered outliers based on knowledge from field surveys. These plots were located in the southwest corner of the site and were identified through an abnormally high soil organic carbon (SOC) content. The four plots had SOC values of 40.8, 49.1, 62.3, and 65.5 g C kg⁻¹, while the mean and standard error for the remaining plots was 8.6 and 0.32 g C kg⁻¹ respectively. The high SOC content was presumably caused by an oil spill in the area. Plots categorized as "other" in the landuse variable were also removed from the data. A total of four plots were classified as "other" and included e.g. school compounds and a high voltage electricity line. Because infiltrability was measured in the upper layer of the soil, the dataset was scaled down to only include the most relevant soil measurements, which was the data for topsoil. An additional reason for reducing the size of the dataset was practicality and to make the study more feasible.

Linear mixed-effects models were used to analyse the effect of the different variables on K_{fs} (general reference on mixed-effects models (Zuur et al. 2009; Bolker et al. 2009). This was deemed the most appropriate modelling approach

due to the hierarchical structure of LDSF data (with plots nested within clusters, and clusters nested within sites) and the need to account for variation in K_{fs} between and within sites. The *lmer* function in the R package "lme4" (Bates et al. 2015) was used to fit random intercept linear-mixed effects models. A series of candidate global models, containing observations from 175 plots across 48 clusters from the three sites, were constructed in order to test which explanatory variables had a significant effect on K_{fs}. First, collinearity between explanatory variables was explored in order to avoid including collinear variables into the same model (Harrison et al. 2018). Collinear predictor variables can increase standard error in models and also prevent assessment of the independent effect of the predictors on the response variable (Quinn & Keough 2002; Harrison et al. 2018). Raw explanatory variables with correlation factors >0.7 suggest that both variables should not be included in the same model (Dromann et al. 2013). Subsequently, 12 different models were constructed with the same level of complexity containing different combinations of covariates. Eight variables remained constant throughout the 12 candidate global models (Table 3). Variables representing vegetation cover were systematically replaced between the models WdCovRate (Landuse, VegStructure, and AvTreeDensity/AvShrubDensity) as they were all correlated. Variables accounting for functional diversity and species richness were also highly correlated and were replaced between models to avoid collinearity (FRic count, FEve count, sing.sp count). A universal model including observations from the three sites was derived based on the 12 candidate models. The same process for selecting the optimal model was used for the three site-specific models as well. The only difference was in the universal model both site and clusters within sites were included as random effects (nested random effects). In the site-specific models, only clusters were added as a random effect. This is because the data for each site-specific model was from individual sites, hence there was no need or possibility of accounting for differences between sites.

Model selection on the covariates was then applied to the 12 candidate global models to obtain 12 candidate optimal models with only significant covariates. This was done using the *step* function in the "lmerTest" package in R (Kuznetsova et al. 2013), which eliminates non-significant covariates in an automated stepwise process.

The 12 candidate optimal models were then compared using the *anova* function in order to derive the Akaike Information Criterion (AIC) scores (Burham & Anderson 2002) for each model. The AIC score is a measure of the relative quality of statistical models and can therefore be applied as a model selection criterion. The model with the lowest AIC score among the 12 candidate optimal models was selected as the optimal model with the best fit (Burham & Anderson 2002). The same process was used to derive optimal models for individual sites, using individual separate datasets from each site.

Significance of fixed-effects in the optimal models was evaluated based on t tests using the Sattherwhite approximation for degrees of freedom (Kuznetsova et al. 2013). A significance level (α) of 0.05 was used. The Satterthwaite method for deriving p-values is suitable for smaller and unbalanced datasets as it results in lower Type 1 error rates as compared to likelihood ratio tests and Wald tests (Luke 2017).

Model diagnostic plots were done using the "sjPlot" package (Lüdecke 2018), and were used for model validation. The "MuMin" package was used to derive $R^2_{conditional}$ and $R^2_{marginal}$ values for fixed and random + fixed effects (Nakagawa & Schielzeth 2012). All statistical analyses were conducted using R statistics (R Core Team 2020).

Number Model 1.1 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + Landuse + sing.sp_count + (1|Site/Cluster) $K_{fs} \sim prepH + predSand + CWM.wd_count + CWM.decid_count + CWM.nfix count +$ 1.2 HerbCovRate + Erosion1b + ImpactGrazing + Landuse + FEve_count + (1|Site/Cluster) 1.3 K_{fs} ~ prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count + HerbCovRate + Erosion1b + ImpactGrazing + Landuse + FRic_count + (1|Site/Cluster) 2.1 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + VegStructure + sing.sp count + (1|Site/Cluster) 2.2 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + VegStructure + FEve_count + (1|Site/Cluster) 2.3 HerbCovRate + Erosion1b + ImpactGrazing + VegStructure + FRic_count + (1|Site/Cluster) 3.1 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + WdCovRate + sing.sp count + (1|Site/Cluster) 3.2 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + WdCovRate + FEve_count + (1|Site/Cluster) $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ 3.3 HerbCovRate + Erosion1b + ImpactGrazing + WdCovRate + FRic_count + (1|Site/Cluster) 4.1 K_{fs} ~ prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count + HerbCovRate + Erosion1b + ImpactGrazing + AvTreeDensity + AvShrubDensity + sing.sp_count + (1|Site/Cluster) 4.2 $K_{fs} \sim prepH + predSand + CWM.wd count + CWM.decid count + CWM.nfix count +$ HerbCovRate + Erosion1b + ImpactGrazing + AvTreeDensity + AvShrubDensity + FEve count + (1|Site/Cluster) 4.3 $K_{fs} \sim prepH + predSand + CWM.wd_count + CWM.decid_count + CWM.nfix_count +$ HerbCovRate + Erosion1b + ImpactGrazing + AvTreeDensity + AvShrubDensity + **FRic_count** + (1|Site/Cluster)

Table 3. List of the 12 candidate global linear mixed-effects models tested to derive the optimal model explaining K_{fs} across sites. The same series of models was used for site-specific modelling (with a modified random structure including only clusters).

3. Results

3.1. Site Characterisation

3.1.1. Soil Properties

Topsoil properties varied strongly between sites and followed a repeating trend, with Muminji consistently showing intermediate values between those from Kubo South and Thange (*Figure 3*). Median K_{fs} in Kubo South was 102 mm h⁻¹; more than twice as high as in Muminji and Thange (44.9 and 34.5 mm h⁻¹, respectively). Median sand content was also highest in Kubo South (59.1%), followed by Muminji (47.5%) and then Thange (31.2%). In contrast, SOC concentration followed the opposite trend; median SOC was lowest in Kubo South (5.2 g C kg⁻¹) and highest in Thange (9.8 g C kg⁻¹). There was a strong negative correlation between SOC and sand content (Pearson correlation coefficient = -0.7; *Appendix Figure 1*). pH values indicate that Kubo South has mostly acidic soils, while the soils in Thange are mostly alkali.



Figure 3. Boxplots of soil properties for the three sites. A) Topsoil field-saturated hydraulic conductivity (K_{fs} , mm h^{-1}); B) Topsoil sand content (%); C) Topsoil organic carbon concentration (g kg⁻¹); D) Topsoil pH.

3.1.2. Land Use and Land Degradation

The land degradation and landuse variables also indicate large differences between sites (Figure 4). Muminji was the site with highest erosion prevalence, with 58% of the plots showing signs of erosion, followed by Thange (33%). In Kubo South only 9% of plots showed signs of erosion. The impact of grazing also varied between sites. Overall, Kubo South and Thange showed lower signs of grazing impact than Muminji. Muminji had a greater quantity of plots showing severe and high grazing impact (39%). The landuse patterns also illustrate site differences. The majority of plots in Kubo South were categorized as annual cropland with agroforestry (41%), followed by fallow land (22%) and perennial cropland (13%). Contrastingly, the dominant land use class in Muminji was closed rangeland (26%), followed by fallow land (24%) and annual cropland (15%). In Thange, the most common land use classes were annual cropland (40%), annual cropland with agroforestry (17%), fallow land (17%) and closed rangeland (17%). The pattern of grazing impact coincides with the higher amount of plots categorized as open and closed rangeland in Muminji. Kubo South and Thange appear to have more land designated for crop production, while Muminji



had a larger percentage of rangeland and fallow plots in comparison to the other sites.

Figure 4. Relative frequency bar charts for different variables related to land degradation and landuse across the three sites. In clockwise order: A) Presence / absence of visible signs of erosion within subplot 1 (sheet, rill or gully). B) Impact of grazing, ranging from 0 (none) to 3 (severe). C) Landuse class.

3.1.3. Vegetation Cover

Vegetation cover was different between sites in terms of aboveground woody biomass, total vegetation cover (total herbaceous and woody cover) and structure (*Figure 5*). Kubo South had the highest median total aboveground woody biomass (401.8 kg), while Muminji and Thange had lower values (97.4 and 65.8 kg, respectively). Median total vegetation cover was highest in Kubo South and lowest in Thange. The range of vegetation cover was highest in Kubo South, which indicates occurrence of plots with both very high and low vegetation cover, whereas in Muminji and Thange the range was lower. The most common vegetation structures were the same across the three sites: bushland, cropland and shrubland. However, their relative occurrence varied among sites. The main distinction between Kubo South and Muminji was that Muminj had markedly



more shrubland (32% vs. 17%). In Thange, in contrast, most of the plots (62%) were classified as cropland.

Figure 5. Graphs showing differences in vegetation cover and vegetation structure among the three sites. A) Boxplot of total aboveground woody biomass (kg) with a log_{10} scale for biomass; B) Boxplot of total vegetation cover (both herb and woody cover) based on a rating scale ranging from 0 (bare) to 5 (>65%); C) Relative frequency bar graph of vegetation structure classes.

3.1.4. Functional Properties of Woody Vegetation

The sites also differed in terms of woody vegetation functional properties (*Figure* 6) and species richness (*Appendix Figure 2*, *Appendix Figure 3* and *Appendix Figure 4*), most notably when comparing functional evenness and functionally singular species, although all functional diversity indices were strongly related (*Appendix Figure 5*). Functional evenness was highest in Kubo South, followed by Thange and Muminji. The higher interquartile range (IQR) for functional evenness in Thange (0 - 0.8) and Muminji (0 - 0.7) in comparison to Kubo South (0.59 - 0.86) is caused by a higher amount of plots containing <2 functionally singular species (which results in a functional evenness score of 0). Kubo South also had the highest median and the greatest IQR for functionally singular species, while Thange had the lowest. The median value for community-weighted mean (CWM) was relatively similar for wood density, albeit with a slightly higher median in Muminji (wd = 0.7 g/cm³) in comparison to Kubo South (wd = 0.6

g/cm³) and Thange (wd = 0.6 g/cm³). The median value CWM for SLA was relatively similar between sites and differed only by 1 mm² mg⁻¹. For the CWM of deciduousness, >50% of plots in all sites were dominated by evergreen species, with the highest percentage in Muminji (71%). The CWM for nitrogen fixation shows that nitrogen-fixing trees dominated a low percentage of plots in all sites: 7% in Kubo South, 8% in Muminji and 21% in Thange.



Figure 6. Graphs showing differences in woody vegetation functional properties among the three sites. A) Boxplots of functional evenness. B) Boxplots of quantity of functionally singular species. C) Boxplots of CWMs of wood density. D) Boxplots of CWMs of specific leaf area. E) Relative frequency bar chart of CWM for deciduousness, where 0 = evergreen, 0.5 = semi-deciduous and 1 = deciduous. F) Relative frequency bar chart of CWM for nitrogen fixation, where 0 = non-nitrogen fixing and 1 = nitrogen fixing.

3.2. Models

3.2.1. Optimal Model Across Sites

The variables that best explained the variation in K_{fs} across the three sites were topsoil sand content, presence of erosion, the perennial cropland land use class and FEve of woody vegetation, according to the optimal model (*Table 4*). Results

from this model indicate that topsoil sand content and Feve both had significant positive effects on K_{fs} . The presence of erosion in subplot 1, where infiltration was measured, had a significant negative effect on K_{fs} . Landuse class also had a significant effect on K_{fs} , with perennial cropland showing significantly higher K_{fs} than annual cropland. The marginal R^2 (which describes the proportion of variance explained by the fixed factor(s) alone) was 0.21, while the conditional R^2 (which describes the proportion of variance explained by both the fixed and random factors) was 0.36.

Table 4. Statistics for fixed effects of the optimal universal model explaining K_{fs} across all sites. Site and clusters within sites were included as random effects in the model (random intercept model). The columns show estimates of the fixed effects (beta values), degrees of freedom, 95% confidence intervals, and p-values (t-tests using Satterthwaite's method). Satterthewaite's tests the null hypothesis stating that $\beta_n = 0$ (i.e. the effect of the fixed effect on $K_{fs} = 0$). The null hypothesis is rejected when $\beta_n \neq 0$. The significant codes for p - values are: <0.05 = *, <0.01 =** and <0.001 = ***. Note that for factor variables, the effect (and corresponding p-values) of the different levels of the variables is shown in comparison to that of the baseline or reference level (i.e., 0 in the case of Erosion, and annual cropland in the case of Land use class).

Predictor	Estimate	DF	СІ	p-Value
(Intercept)	22.7	7.1	-11.2 - 56.62	0.230
Sand Content	1.0	100.4	0.48 - 1.50	<0.001***
Erosion	-16.4	162.0	-30.512.34	0.024*
Land Use: Annual Cropland	-6.6	163.7	-29.83 - 16.64	0.579
with Agroforestry				
Land Use: Fallow	-18.1	163.0	-40.04 - 3.84	0.108
Land Use: Perennial Cropland	28.1	162.3	2.68 - 53.51	0.032*
Land Use: Perennial Cropland	-3.9	163.6	-35.89 - 28.17	0.813
with Agroforestry				
Land Use: Closed Rangeland	-8.0	162.7	-32.08 - 16.16	0.518
Land Use: Open Rangeland	-19.4	158.2	-50.92 - 12.11	0.229
Functional Evenness	20.4	163.4	0.82 - 40.03	0.043*

Because the factor variables included in the model, erosion and landuse, have two and seven classes respectively, the optimal model consists of 14 different equations. These equations represent a mean between the three different sites, which can be referred to as a typical site. The 14 equations are visually represented in *Figure 7* and *Figure 8* (K_{fs} vs. sand and functional evenness, respectively). As shown in *Table 3*, plots showing signs of erosion had an overall lower K_{fs}. Predicted K_{fs} also differs between land use classes. The perennial cropland falls outside the confidence interval of annual cropland and has a significant positive effect on K_{fs} compared to the other classes.



Figure 7. Predicted topsoil field-saturated hydraulic conductivity (K_{fs}) as a function of sand content, average FEve index across sites, presence of erosion and land use class for a typical site and cluster. The envelopes represent the 95% confidence intervals for the predicted K_{fs} values corresponding to annual cropland (baseline level). The left graph shows the predicted K_{fs} values under conditions when there are no signs of erosion, whereas the right graph shows predicted K_{fs} for eroded soils.



Figure 8. Predicted topsoil field-saturated hydraulic conductivity (K_{fs}) as a function of functional evenness (FEve index), average sand content across sites, presence of erosion and land use class for a typical site and cluster. The envelopes represent the 95% confidence intervals for the predicted K_{fs} values corresponding to annual cropland (baseline level). The left graph shows the predicted K_{fs} values under conditions when there are no signs of erosion, whereas the right graph shows predicted K_{fs} for eroded soils.

Figure 9 shows a graphical representation of the random variable site on K_{fs} . The optimal model predicts a higher K_{fs} in Kubo South, and a lower K_{fs} in Muminji and Thange. The differences in y-intercept of the lines illustrate the impact of the random effects of the different sites on K_{fs} .



Figure 9. Predicted topsoil field-saturated hydraulic conductivity (K_{fs}) as a function of sand content for a typical site and cluster when there is no erosion and land use is annual cropland (baseline equation, black line). The coloured lines illustrate the effect of the random variable Site on K_{fs} .

3.2.2. Site-specific Models

The optimal models for each individual site contained different variables and combinations in comparison to the optimal model for all sites. The optimal models for Kubo South and Muminji were relatively simple as they only contained one fixed effect, sand content and erosion, respectively (*Table 5* and *Table 6*). As in the optimal model for the three sites, sand content had a significant positive effect on K_{fs} , whereas erosion had a significant negative effect. The optimal model for Thange was more complex and contained three variables: erosion, Impact Grazing and Landuse (*Table 7*). Both land use classes closed rangeland and perennial cropland had a significant positive effects on K_{fs} compared to the baseline level (annual cropland). Impact grazing, on the other hand, had a significant negative effect on K_{fs} . In contrast to the optimal model for the three sites and the site-specific model for Muminji, erosion had a significant positive effect on K_{fs} . After examining the relationship between presence of
erosion and sand content in Thange and realizing that the eroded sites contained markedly higher sand content (*Appendix Figure 6*), another model was run without erosion as a covariate (*Table 8*). In the revised model, sand content replaced erosion, and along with perennial cropland and closed rangeland, had a positive effect on K_{fs}, while grazing negatively affected K_{fs}. In Muminji, more of the variance was explained by combined fixed and random effects ($R^2_{conditional} = 0.15$), as opposed to only fixed effects ($R^2_{marginal} = 0.17$) or in the revised Thange model ($R^2_{marginal} = 0.712$).

Table 5. Statistics for fixed effects for optimal model explaining K_{fs} in Kubo South. Clusters were included as a random effect in the model. The columns show beta estimates of the fixed effects (beta values), degrees of freedom, confidence interval and p-value (Satterthwaite). The significant codes for p - values are: <0.05 = *, <0.01 = ** and <0.001 = ***.

Predictor	Estimate	DF	CI	p-Value
Intercept	-39.5	44.0	-138.0 - 59.1	0.436
Sand Content	2.5	44.0	0.9 - 4.2	0.004**

Table 6. Statistics for fixed effects for optimal model explaining K_{fs} in Muminji. Clusters were included as a random effect in the model. The columns show beta estimates of the fixed effects (beta values), degrees of freedom, confidence interval and p-value (Satterthwaite). The significant codes for p - values are: <0.05 = *, <0.01 = ** and <0.001 = ***.

Predictor	Estimate	DF	СІ	p-Value
Intercept	68.1	40.5	54.9 - 81.3	< 0.001 ***
Erosion	-26.6	85.0	-43.110.1	0.002**

Table 7. Statistics for fixed effects for optimal model explaining K_{fs} in Thange. Clusters were included as a random effect in the model. The columns show beta estimates of the fixed effects (beta values), degrees of freedom, confidence interval and p-value (Satterthwaite). The significant codes for p - values are: <0.05 = *, <0.01 = ** and <0.001 = ***.

Predictor	Estimate	DF	СІ	p-Value
Intercept	28.5	33	-13.1 - 52.3	<0.001***
Erosion	14.4	33	0.5 - 1.6	0.006**
Impact Grazing	-12.1	33	-30.62.6	0.006**
Land use: Annual cropland	10.8	33	-30.8 - 13.7	0.088
with agroforestry				
Land use: Fallow	12.0	33	-38.7 - 5.1	0.201
Land use: Perennial cropland	47.6	33	8.5 - 59.3	0.002**
Land use: Perennial cropland	10.8	33	-33.4 - 35.9	0.431
with agroforestry				
Land use: Closed rangeland	61.9	33	-34.3 - 13.9	<0.001***
Land use: Open rangeland	13.1	33	-51.1 - 11.4	0.372

Table 8. Statistics for fixed effects for revised optimal model explaining K_{fs} in Thange. Clusters were included as a random effect in the model. The columns show beta estimates of the fixed effects (beta values), degrees of freedom, confidence interval and p-value (Satterthwaite). The significant codes for p - values are: <0.05 = *, <0.01 = ** and <0.001 = ***.

Predictor	Estimate	DF	СІ	p-value
Intercept	17.2	33	-5.01 - 29.33	0.009**
Sand Content	0.5	33	0.13 - 0.89	0.013*
Impact Grazing	-13.3	33	-21.964.55	0.005**
Land use: Annual cropland with agroforestry	8.0	33	-4.08 - 20.17	0.203
Land use: Fallow	16.8	33	-2.25 - 35.90	0.093
Land use: Perennial cropland	37.3	33	9.66 - 65.03	0.012*
Land use: Perennial cropland with agroforestry	3.2	33	-24.25 - 30.68	0.82
Landuse: Closed rangeland	64.9	33	47.91 - 81.87	<0.001***
Landuse: Open rangeland	24.0	33	-7.35 - 55.44	0.143

4. Discussion

Understanding what factors affect topsoil saturated hydraulic conductivity across different landscapes is important for identifying areas where provision of hydrological ecosystem services is low. Deepening this understanding would also improve identification and application of land management as well as restoration practices that maintain or enhance soil hydrological function. The outcomes of the optimal linear mixed-effects model showed that the key variables in explaining K_{fs} across the three studied landscapes were sand content, erosion, FEve of woody vegetation and land use. The results align with the stated hypotheses; that K_{fs} is affected by inherent soil properties, vegetation cover and functional diversity of woody plants. However, direct measurements of woody vegetation, such as woody biomass and density, had no significant effects on K_{fs} . The positive effects of woody vegetation were captured in other variables such as landuse and functional evenness.

4.1. Inherent Soil Properties

The optimal mixed-effects model showed that sand content explained most of the variation in K_{fs} across sites. This is not surprising as the sites exhibited extreme ranges in sand content, and supports the hypothesis of this study. The strong linkage between K_{fs} and soil texture is well documented (Hillel 1980; Ma et al. 2016; García-Gutiérrez et al. 2017), and sand content is a reflection of this relationship. Increased sand content is indicative of coarser soil texture, which has a positive effect on K_{fs} . As Kubo South had sandier soils than the other sites, it is reasonable that it exhibited the highest K_{fs} . In contrast, Thange, where the soils were more fine-textured, had lower K_{fs} values. Fine-textured soils not only have smaller pores, but these can be further reduced in size during rainfall due to swelling of clay particles (Medinski et al. 2009). However, it should also be noted that Kubo South contained other site properties conducive to a higher K_{fs} , such as more vegetation and lower rates of both erosion and grazing.

After revising the model and removing erosion as a covariate in the sitespecific optimal model for Thange, a combination of sand content, grazing impact and land use were significant and explained the variance in K_{fs} between clusters. The addition of sand content to the revised optimal model supports the assumption that the initial positive effect of erosion on K_{fs} , in the first model, was caused by negative correlation between erosion and sand content. This suggests that in fine-grained soils, with low sand content, other factors are also important in driving differences in K_{fs} . This contrasts the results from the site-specific model in Kubo South, in which sand content was the only explanatory fixed effect. This may indicate that sand content is the dominant factor affecting K_{fs} , which coincides with other studies emphasizing the strong effect of texture on infiltrability (Blackburn 1975; Mills et al. 2006; Medinski et al. 2009).

Other soil property variables that can affect K_{fs} , such as SOC, were excluded from the model. SOC has been shown to improve soil aggregation and structure (Franzluebbers 2002; Lado et al. 2004; Hao et al. 2020) and its reduction is linked to a dampened soil water holding capacity (Valentin & Bresson 1997; Lal et al. 2004). Research has demonstrated that SOC is strongly negatively affected by sand content, due to higher rates of microbial degradation (Jobbágy & Jackson 2000; Vågen & Winowiecki 2013), which supports the observed correlation between the two variables in this study. Soils with high clay content tend to have more SOC as clay particles stabilize soil structures and protect organic matter from degradation (Jobbágy & Jackson 2000). The large range in sand content resulted in a clear SOC gradient between sites, which could have clouded the effect of SOC on K_{fs} and hindered determination of statistical significance between SOC and K_{fs} in the model. Mills et al. (2006) noted a lower infiltrability in soils with high SOC and N, which was explained by a greater absorption of organic content in fine-grained soils than soils with coarser texture. Hence, the driving factor of K_{fs} was not organic matter, rather it was texture. Studies such as Mills et al. (2006) demonstrate the difficulty in distinguishing between correlation and causality in ecological studies. This challenge is compounded for observational research in comparison to experimental studies (Larsen et al. 2019). This dilemma reinforces the need for additional data to draw further conclusions concerning the relationship between SOC and K_{fs}. Therefore, more data is needed from sites with more narrow ranges in sand content in order to elucidate the potential effect of SOC on K_{fs} through comparing sites with similar soil properties.

4.2. Land Degradation

The modelling results showed that the presence of erosion, which is a proxy for land degradation, had a negative effect on K_{fs} across the three sites. Soil erosion can result in the loss of SOC and overall reduced soil health (Dregne 2002; Vågen & Winowiecki 2013; Lohbeck et al. 2017). SOC and soil aggregation are strongly linked to infiltrability (Franzluebbers 2002), which could explain why the optimal model indicates that more eroded soils have lower K_{fs} . Erosion also impacts the

soil-water relationship through damaging the soil structure, which reduces soil porosity and increasing rates of crusting (Bossio et al. 2009).

It is noteworthy that of the erosion variables that were part of the initial dataset, the binary classification of presence or no presence of erosion best explained variance in K_{fs} across the sites. When the binary erosion variable in the optimal universal model was exchanged for an erosion variable using a scale of 0-4, erosion was no longer significant. Therefore, this suggests that the severity of erosion is not relevant for explaining K_{fs} . Rather, it is the mere presence of erosion which is important. This indicates that any signs of erosion, regardless of how severe, will have a negative impact on K_{fs} . However, a limitation with the dataset is that Kubo South, which had the highest median K_{fs} , also had the lowest percentage of erosion is relevant in sites with different soil conditions. Furthermore, the erosion variable based on the severity scale may have proved more relevant with additional sites, in order to distinguish if greater erosion intensity leads to reduced infiltrability.

Grazing impact, which is another proxy for land degradation, had a negative effect on K_{fs} in the optimal site-specific model for Thange. Other studies have also found that grazing reduces rates of infiltration (Gifford & Hawkins 1978; Mwendera & Saleem 1997; Basche & Delonge 2019; Marquart et al. 2020). This could be caused by livestock trampling increasing soil compaction (Greenwood & McKenzie 2001) or by overgrazing causing desertification through reduced perennial grass cover (Castellano & Valone 2007; Basche & Delonge 2019). The reduction in vegetation cover leads to less organic matter content and increased bulk density, which leads to decreased infiltration rates. Therefore, the statistical significance of grazing impact in the optimal model for Thange is in accordance with previous research.

Soil erosion was the sole factor in the optimal site-specific model for Muminji. Muminji contained a higher proportion of sites showing signs of erosion, which could suggest that erosion is the dominating factor for reduced K_{fs} in sites exposed to high amounts of land degradation. It is also important to note that distinguishing the cause-effect relationship between erosion and infiltrability is difficult. The soils could have an inherently low SOC content, and therefore be more prone to erosion leading to reduced K_{fs} . Alternatively, soil erosion, caused by activities such as overgrazing or trampling by cattle (Marquart et al. 2020), could lead to a loss in SOC and a subsequent reduction in K_{fs} . Regardless, it is clear that, in this study, eroded soils had lower rates of K_{fs} due to different processes negatively affecting soil hydraulic properties.

4.3. Woody Functional Diversity

The optimal model showed that functional diversity of woody vegetation had a positive effect on K_{fs} , suggesting that a more functionally diverse woody vegetation cover improves soil hydraulic properties. This is in accordance with the hypothesis of this study. One explanation for this relationship are the complex interactions between soil properties and woody plant functional diversity, including the added input of organic matter boosting soil porosity and leading to more soil aggregation (Mando et al. 1996; Ilstedt et al. 2007), as well as increased macropores created by root systems and associated macrofauna (Bargués Tobella et al. 2014; Fischer et al. 2015). More specifically, evenness of species and their functional strategies may increase microhabitats in soils through maximizing the amount of root volume (Lamb et al. 2011). Mensah et al. (2020) found a positive relationship between functional evenness and aboveground biomass caused by more effective resource utilization. Improved resource utilization will lead to greater productivity in ecosystems, which in turn leads to more biomass.

Other studies have found similar relationships between different measures of functional diversity and ecosystem functioning. Liu et al. (2019) found a positive effect of plant species diversity on infiltration capacity in soils, citing the heightened community productivity of diverse ecosystems leading to more organic matter input increasing aggregation and soil porosity. The positive effect of diversity on infiltration rates in this study could be two-fold, as the aforementioned factors directly improve K_{fs} through affecting soil properties while simultaneously decreasing erosion. Zhu et al. (2015) found a strong negative relationship between functional diversity and erosion, which supports this conclusion. However, this relationship was not observed for functional evenness, and was best described by functional divergence (Zhu et al. 2015).

A central question for understanding how biodiversity affects ecosystems functioning is identifying which aspect of biodiversity exerts the greatest influence on ecosystem processes (Cadotte et al. 2009). The inclusion of multiple measures of functional diversity in this study allowed for an identification of the most important measure for the specific sites in the dataset. Each FD measure accentuates a different facet of biodiversity. Functional evenness describes how regular the distribution of functional traits in a community (plot) are, and previous studies have illustrated the strong link between functional evenness and multifunctionality (Bagousse-Pinguet et al. 2021). FEve is affected more by the abundance of species in comparison to FRic, which is more dependent on species richness (Magnago et al. 2014). The fact that FEve has a stronger effect than FRic in this study suggests that K_{fs} is, to a greater extent, driven by the distribution and abundance of functionally singular species as opposed to their mere quantity. Based on this, management decisions aiming to restore soil hydraulic properties may benefit from focusing on the distribution of different woody species in an ecosystem, as opposed to promoting rare or singular species that contain highly diverging functional traits. Although this inference is limited to the three sites included in this study, it can have consequences for management decisions concerning the promotion and planting of woody species in tropical ecosystems.

However, it should also be noted that research concerning the effect of functional diversity on soil hydraulic properties is severely limited. The effect of woody species FD on ecosystem functioning in general is poorly understood, as studies have reached different conclusions. For example, although Mensah et al. (2020) found a positive relationship between FEve and aboveground biomass, Finegan et al. (2015) did not. A reason for differing conclusions concerning specifically FEve may be caused by the index itself. Some more recent studies have questioned the validity of the index (Legras & Gartner 2018; Kosman et al. 2021), in part due to FEve index values being derived from a combination of functional distance (differences in functional traits between species) and abundance distribution of species. The simplification of two different metrics into one value inherently leads to loss of information.

Due to the variety of different interpretations of FD indices and how they affect productivity, a tentative conclusion from this study is that FEve plays an important role in driving K_{fs} . However, this conclusion is drawn with caution, in part due to the multitude of different interpretations of FD indices and how they affect productivity in ecosystems. Nevertheless, the presence of FEve in the optimal model for describing variation in K_{fs} across the three sites merits further investigation into the role of functional diversity in driving soil hydraulic properties. With regard to contrasting research and opinion concerning different measures FD, in particular FEve, additional research is needed to unequivocally identify the specific role of functional diversity on infiltrability.

A limitation of this study was the inclusion of only four common functional traits. Although information concerning these traits was available from public databases, data on less common and rare tropical species was scarce. Therefore, genus- and family-based medians had to be used. However, this may contribute to inaccuracies for certain species, as functional traits such as wood density and deciduousness can differ between regions and within genus/family. Future research on ecosystem function and functional traits would benefit from field studies where traits are measured and quantified based on local conditions and species. Furthermore, studies focusing on infiltrability and FD may include more relevant traits to soil hydraulic properties. Research has shown positive relationships between infiltrability and fine root length density (Hao et al. 2020) and root biomass (Leung et al. 2018). These findings, along with the observed positive effect of FEve on K_{fs} in this study also merits future research concerning the effects of functional diversity on infiltrability.

4.4. Land Use

The positive effect of vegetation quantity on K_{fs} was captured by land use in the optimal universal model across sites and the site-specific model in Thange. Fixed effects predictors included in the model tests that represented woody vegetation quantity, such as tree density and woody cover variables, were all eliminated from the model due to low statistical significance. This contrasts with previous research that has shown strong positive relationships between K_{fs} and tree cover (Ilstedt et al. 2007; Bargués Tobella et al. 2014; Bonnesoeur et al. 2019). However, the exclusion of the woody vegetation quantity variables from the optimal model does not necessarily suggest a lack of effect of trees on K_{fs}. As multiple classes in the land use variable are based on the quantity of vegetation, such as open and closed rangeland, the land use variable reflects the amount of vegetation in the plot as well. The land use variable also indirectly includes non-woody plants, such as annual crops, which have an effect on infiltrability. Therefore, the quantity of woody vegetation, both in terms of biomass and cover, was encapsulated in the land use variable and had a greater explanatory effect on K_{fs} in the optimal model than the direct measurements of woody cover and tree/shrub density.

Perennial cropland had significantly higher K_{fs} than annual cropland, while the remaining classes fall within the confidence interval for the annual crop class, thus preventing conclusions to be drawn concerning differences in effect on K_{fs} for these land use classes. This could be due to an unbalanced sample size, for example there were only nine plots categorized as perennial cropland with agroforestry and 34 as annual cropland with agroforestry (total plots = 175). Nonetheless, K_{fs} for perennial cropland differed significantly from that for annual cropland (baseline level), which is most likely due to the types of crops cultivated. Crops categorized as perennial in the dataset include khat, cashew and pigeon peas. Previous studies have found a positive effect of perennial crops such as alfalfa on K_{fs}, due to the roots reforming channels in soils after tillage and through bioturbation by their roots (Meek et al. 1992; Huang et al. 2019). Basche & Delonge (2019) performed a meta-analysis comparing conventional agricultural methods and alternative agricultural and found a consistent positive impact of perennial crops and agroforestry systems in comparison to conventional crop systems, such as annual crops, on rates of infiltration.

The distinguishing characteristic of perennials is that they create continuous roots over time in soil and provide a semi-permanent soil cover. The presence of roots has been found to increase infiltration rates into soil through creating macropores that enhance preferential flow (van Schaik 2009; Zhu et al. 2015). Maintaining a continuous cover of vegetation, through for example cultivating perennials, is associated with reduced soil disturbance and increased biological activity (Basche & Delonge 2019). Less soil disturbance through minimal tillage has been found to massively increase earthworm activity (Briones & Schmidt et

al. 2017), a species that has a documented positive effect on infiltrability through increasing macroporosity (van Schaik et al. 2014; Fischer et al. 2014). Hence, these factors may contribute to the higher K_{fs} associated with perennial croplands observed across the three sites. The site-specific optimal model in Thange showed a significant effect of both perennial cropland and closed rangeland. In this study, closed rangelands were defined as land mainly used for grazing with a vegetation structure of bushland, wooded grassland, woodland or thicket, and hence contain a higher woody vegetation cover than open rangeland. These site-specific results, and the significant effect of perennial crops in the universal optimal model for the three sites, support the hypothesized positive relationship between increased woody vegetation and K_{fs} .

Several problems arose when classifying plots based on land use that complicated classification and could be improved in future studies. Plots containing both annual and perennial crops were classified differently based on the quantity of cultivated perennial and annual species. Without data concerning the cover of specific crops, this classification becomes rudimentary and may not be representative of the differences in vegetation cover between plots and their associated properties, such as woody/non-woody, annual/perennial cropland or shrub/tree cover. In addition, more specific definitions for perennial crops would be advisable for future studies incorporating land use. For example, crop trees, such as cashew and citrus, were classified as perennial crops. These perennial crops are markedly different from pigeon peas and khat, and will have dissimilar functional properties, such as root structures and wood density, as they are trees and not small shrubs or perennial plants. Therefore, classifying species based on annual/perennial qualities may be too simple - including a binary classification if perennial crops are trees or not could make the land use variable more accurate. Furthermore, classification of agroforestry systems involves considerable qualitative analysis based on fieldwork observations, which cannot always be captured with data concerning tree cover.

5. Conclusion

The results from this study indicate that sand content, functional diversity, land degradation and land use drive K_{fs} across the three studied landscapes. The sitespecific models provided more insight into how the impact of these variables changed under more uniform conditions. In Thange, where the soils were in general more fine-grained, the effect of sand content on K_{fs} was reduced but still significant. Instead, land use and grazing had a larger role in explaining K_{fs}. These findings suggest that efforts to restore soil hydraulic functioning in fine-grained soils may benefit from focusing on promoting continuous vegetation cover through for example perennial crops, more woody vegetation and managing livestock grazing to reduce the negative effects of overgrazing and soil compaction on infiltration. Results also indicate that in sandier soils, where K_{fs} is inherently high, there is no real need to restore soil hydrological functioning. Furthermore, degraded land across the sites had a lower K_{fs}, which suggests that management practices that minimise and reverse land degradation could have positive effect on K_{fs}. However, these conclusions are based on the specific combination factors contained in this study. If an optimal universal model was derived for a different set of sites, other factors may be dominant in driving infiltrability on the landscape scale.

Future studies examining landscape-level drivers of K_{fs} should include more sites to have a larger sample size leading to more combinations of variables such as land use and texture which would allow comparison of sites with more uniform conditions. This approach could also be simulated in an experimental or controlled study, where the study design could control for variables such as sand content or land use. An increased sample size would expand upon the results of this study and provide more insight into the how the relationship between vegetation and K_{fs} differs across sites with varying soil textures.

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8. Appendix

Variable	Variable Measureme nt Scale	Units	Description
VegStructure	Plot	-	Vegetation structure based on 7 classes: bushland, cropland, grassland, shrubland, thicket, wooded grassland, woodland.
Landuse	Plot	-	Land use based on 10 classes: annual agroforestry, annual crop, fallow, other, pasture rangeland (closed), pasture rangeland (closed), perennial agroforestry, perennial crop.
ImpactAgric	Plot	0 - 3 (rating scale)	Impact rating of agriculture.
ImpactErosion	Plot	0 - 3 (rating scale)	Impact rating of erosion.
Treeagb	Plot	kg	Total biomass of trees.
Shrubagb	Plot	kg	Total biomass of shrubs.
Woodyagb	Plot	kg	Total woody biomass.
HerbCovRate	Plot	0 - 5 (rating scale)	Herbaceous cover rating based on Braun- Blanquet (1928), 0 = bare and 5 = >65% cover.
WdCovRate	Plot	0 - 5 (rating scale)	Woody cover rating based on Braun-Blanquet (1928), 0 = bare and 5 = >65% cover.
VgCovRate	Plot	0 - 5 (rating scale)	Total vegetation cover rating based on Braun- Blanquet (1928), 0 = bare and 5 = >65% cover.
TD1	Subplot	Trees ha ⁻¹	Tree density in subplot 1.
SD1	Subplot	Shrubs ha ⁻¹	Shrub density in subplot 1.
WD1	Subplot	Woody ha ⁻¹	Density of woody vegetation in subplot 1.
Erosion1b	Subplot	0 - 1 (binary)	Erosion in subplot 1
K _{fs}	Subplot	mm h ⁻¹	Field-saturated hydraulic conductivity
AvTreeDensity	Plot	Trees ha ⁻¹	Average tree density
AvShrubDensity	Plot	Shrubs ha ⁻¹	Average shrub density
Texture_newclass	Plot	-	Texture of topsoil (sandy, silty or clay)
predSOC	Plot	g kg ⁻¹	Topsoil soil organic carbon content
predTN	Plot	g kg ⁻¹	Topsoil nitrogen content
predpH	Plot	pН	Topsoil pH

Appendix Table 1. Complete list of variables and corresponding units included in datatset.

predExBas	Plot	mmol kg ⁻¹	Topsoil exchangeable bases	
predSand	Plot	%	Topsoil sand content	
predClay	Plot	%	Topsoil clay content	
sing.sp	Plot	n (species)	Functionally singular species	
FRic	Plot	0 -1 (index)	Functional richness	
FEve	Plot	0 -1 (index)	Funtional evenness	
FDiv	Plot	0 -1 (index)	Functional diversity	
FDis	Plot	0 -1 (index)	Functional dispersion	
RaoQ	Plot	0 -1 (index)	Rao's Quadratic Entropy	
CWM.wd	Plot	Wood Density (g cm ³)	Community-weighted mean wood density	
CWM.decid	Plot	0, 0.5, 1 (scale)	Community-weighted mean deciduousness	
CWM.nfix	Plot	0 - 1 (binary)	Community-weighted mean nitrogen fixation	
CWM.sla	Plot	Specific Leaf Area (mm ² mg ⁻¹)	Community-weighted mean specific leaf area	



Appendix Figure 1. Scatterplot showing relationship between SOC and sand content across all plots included in the filtered dataset used for modelling purposes.



Appendix Figure 2. Bar chart showing species abundance, based on count, of 50 most common species in Kubo South.



Appendix Figure 3. Bar chart showing species abundance, based on count, of 50 most common species in Muminji.



Appendix Figure 4. Bar chart showing species abundance, based on count, of 50 most common species in Thange.



Appendix Figure 5. Results from colinearity test of functional diversity variables. Variables with ≥ 0.7 in correlation factor should not be included in the same model.



Appendix Figure 6. Differences in sand content across sites in eroded and non-eroded soils. Erosion is measured in subplot 1, 0 = no signs of erosion, 1 = signs of erosion (rill, sheet or gully).

Appendix Table 2. Wood density values for all woody species across sites. When multiple sources were used a median wood density was calculated. NA is given when no wood density value was available. Accuracy column reflects how specific the wood density values are for each species: 0 = Africa species-specific; 1 = Global species-specific; 2 = Africa genus-specific; 3 = Global genus-specific; 4 = Africa family-specific; 5 = Global family-specific.

Species	Median Wood Density (g cm ⁻³)	Accuracy	Source
Acacia drepanolobium	0.768	2	Zanne et al. (2009)
Acacia hockii	0.717	0	Mens (2020)
Acacia mellifera	0.893	0	Mens (2020)
Acacia nilotica	0.978	0	Mens (2020)
Acacia nubica	0.768	2	Zanne et al. (2009)
Acacia senegal	0.738	0	Nygård & Elfving (2000) Uganda Forest Department (1992) Vreugdenhil et al. (2012)
Acacia seyal	0.624	0	Uganda Forest Department (1992)
Acacia spp.	0.768	2	Vreugdenhil et al. (2012)

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Artocarpus heterophyllus0.310Uganda Forest Department (1992)Aspilia spp.0.685Zanne et al. (2009)Azadirachta indica0.840Carsan et al. (2012) Uganda Forest Department (1992)Balanites aegyptiaca0.6710Carsan et al. (2012) Nygård & Elfving (2000) Reyes et al. (1992) Uganda Forest Department (1992)Barringtonia racemosa0.5580Carsan et al. (2012) Nygård & Elfving (2012)Bauhinia acuminata0.683Carsan et al. (2012)Observed0.680Carsan et al. (2012)Bauhinia thoningii0.5550Carsan et al. (2012)	Apodytes dimidiata			Carsan et al. (2012)
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Azadirachta indicaImage: Second S	Aspilia spp.	0.68	5	Zanne et al. (2009)
Balanites aegyptiaca0.6710Carsan et al. (2012)Balanites aegyptiaca0.6710Reyes et al. (1992)Balanites aegyptiaca0.6710Reyes et al. (1992)Barringtonia racemosa0.5580Carsan et al. (2012)Bauhinia acuminata0.683Carsan et al. (2012)Bauhinia thoningii0.5650Mens (2020)		0.84	0	Carsan et al. (2012)
Balanites aegyptiacaNygård & Elfving (2000) Reyes et al. (1992) Uganda Forest Department (1992) Vreugdenhil et al. (2012)Barringtonia racemosa0.5580Carsan et al. (2012)Bauhinia acuminata0.683Carsan et al. (2012)Bauhinia thoningii0.5650Mens (2020)	Azadirachta indica			Uganda Forest Department (1992)
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Barringtonia racemosa0.5580Carsan et al. (2012)Bauhinia acuminata0.683Carsan et al. (2012)Bauhinia thoningii0.5650Mens (2020)				Nygård & Elfving (2000)
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Barringtonia racemosa0.5580Carsan et al. (2012)Bauhinia acuminata0.683Carsan et al. (2012)Bauhinia thoningii0.5650Mens (2020)				Uganda Forest Department (1992)
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Bauhinia thoningii 0.565 0 Mens (2020)	Barringtonia racemosa	0.558	0	Carsan et al. (2012)
	Bauhinia acuminata	0.68	3	Carsan et al. (2012)
	Bauhinia thoningii	0.565	0	Mens (2020)
Bixa spp. 0.32 3 Carsan et al. (2012)	Bixa spp.	0.32	3	Carsan et al. (2012)
0.576 0 Carsan et al. (2012)		0.576	0	Carsan et al. (2012)
Blighia unijugata Government of Ethiopia (2016)	Blighia unijugata			Government of Ethiopia (2016)
Uganda Forest Department (1992)				Uganda Forest Department (1992)
Borassus aethiopum 0.975 1 Carsan et al. (2012)	Borassus aethiopum	0.975	1	Carsan et al. (2012)
Boscia angustifolia0.5942Goldsmith & Carter (1981)	Boscia angustifolia	0.594	2	Goldsmith & Carter (1981)
Boscia coriacea0.5942Goldsmith & Carter (1981)	Boscia coriacea	0.594	2	Goldsmith & Carter (1981)
Bourreria petiolaris0.733Barajas-Morales (1987)	Bourreria petiolaris	0.73	3	Barajas-Morales (1987)

Bourreria spp.	0.73	3	Barajas-Morales (1987)
20uii oi iii oppi	0.703	0	Carsan et al. (2012)
Brachystegia spiciformis	0.705		Uganda Forest Department (1992)
Brackenridgea zanguebarica	0.675	3	Carsan et al. (2012)
Bridelia cathartica	0.54	3	Uganda Forest Department (1992)
	0.499	0	Carsan et al. (2012)
Bridelia micrantha			Reyes et al. (1992)
			Uganda Forest Department (1992)
Bridelia spp.	0.54	3	Carsan et al. (2012)
Bridelia taitensis	0.708	0	Mens (2020)
N 1111	0.52	3	Detienne et al. (1982)
Buddleja spp.			Suzuki (1999)
Buttonia spp.	NA	NA	NA
Caesalpinia bonduc	0.875	3	Carsan et al. (2012)
Calotropis procera	0.45	4	Zanne et al. (2009)
Canthium spp.	0.62	3	Carsan et al. (2012)
Capparis tomentosa	0.675	3	Carsan et al. (2012)
Carica papaya	0.188	3	Barajas-Morales (1987)
Carica papaya			Gimenez, A.M. & Moglia, J,G. (2003)
Carissa edulis	0.834	2	Sallenave (1955)
Cassia abbreviata	0.883	0	Goldsmith & Carter (1981)
Cassia afrofistula	0.883	0	Goldsmith & Carter (1981)
Cassia spp.	0.69	3	Carsan et al. (2012)
Cassipourea spp.	0.64	2	Carsan et al. (2012)
Casuarina equisetifolia	1.02	0	Uganda Forest Department (1992)
Catha edulis	0.66	0	Mens (2020)
Chassalia umbraticola	0.65	4	Zanne et al. (2009)
Citrus limon	0.783	0	Mens (2020)
Citrus sinensis	0.74	0	Uganda Forest Department (1992)
Clerodendrum spp.	0.607	2	Desch & Dinwoodie (1996)
			Goldsmith & Carter (1981)
Cocos nucifera	0.5	1	Reyes et al. (1992)
Combretum collinum	0.629	0	Mens (2020)
	0.646	0	Nygård & Elfving (2000)
Combretum fragrans			Uganda Forest Department (1992)
			Goldsmith & Carter (1981)
Combretum molle	0.744	0	Mens (2020)
Combretum schumannii	0.929	0	Carsan et al. (2012)
Combretum spp.	0.8635	2	Carsan et al. (2012)
Combretum zeyheri	0.8635	2	Carsan et al. (2012)

Commiphora africana	0.478	0	Mens (2020)
Commiphora spp.	0.478	2	Carsan et al. (2012)
Commpnora spp.	0.37	0	Carsan et al. (2012)
	0.44	0	Government of Ethiopia (2016)
Cordia africana			1 ()
			Reyes et al. (1992)
	0.02	0	Uganda Forest Department (1992)
Cordia monoica	0.83	0	Uganda Forest Department (1992)
Cremaspora spp.	0.65	4	Zanne et al. (2009)
Crossopteryx febrifuga	0.702	0	Goldsmith & Carter (1981)
Crotalaria agatiflora	0.65	4	Zanne et al. (2009)
Crotalaria spp.	0.65	4	Zanne et al. (2009)
Croton dichogamus	0.951	0	Mens (2020)
Croton megalocarpus	0.62	0	Uganda Forest Department (1992)
Croton spp.	0.57	2	Carsan et al. (2012)
Dalbergia boehmii	0.725	2	Carsan et al. (2012)
	1.08	0	Carsan et al. (2012)
Dalbergia melanoxylon			Nygård & Elfving (2000)
Daibei gia melanoxylon			Uganda Forest Department (1992)
			Vreugdenhil et al. (2012)
Deinbollia spp.	0.802	0	Mens (2020)
Desmodium spp.	0.65	4	Zanne et al. (2009)
	0.854	0	Nygård & Elfving (2000)
Dichrostachys cinerea			Uganda Forest Department (1992)
			Goldsmith & Carter (1981)
Diospyros abyssinica	0.72	0	Carsan et al. (2012)
Diospyros cornii	0.82	2	Reyes et al. (1992)
Diospyros squarrosa	0.8	2	Carsan et al. (2012)
Dodonaea spp.	0.78	3	Carsan et al. (2012)
Dombeya burgessiae	0.482	0	Takahashi (1978)
Dombeya mukole	0.77	0	Uganda Forest Department (1992)
Dombeya spp.	0.5497	3	Carsan et al. (2012)
Dracaena spp.	0.4165	3	Carsan et al. (2012)
Ehretia spp.	0.523	3	Carsan et al. (2012)
	0.525	0	Carsan et al. (1992)
Ekebergia capensis			Government of Ethiopia (2016)
			Uganda Forest Department (1992)
Elaeis guineensis	0.54	5	Zanne et al. (2009)
	0.403	0	Goldsmith & Carter (1981)
Erythrina abyssinica			Uganda Forest Department (1992)
	0.907	0	Carsan et al. (2012)
Erythrophleum suaveolens	0.207		Uganda Forest Department (1992)
			Oganua Poresi Department (1992)

Eucalyptus spp.	0.8266	3	Zanne et al. (2009)
Euclea spp.	0.775	2	Goldsmith & Carter (1981)
Euclea spp.	0.466	3	Benthall (1984)
Funharkia hugasi	0.400	5	Goldsmith & Carter (1981)
Euphorbia bussei			
T 1. 1'	0.220	0	Barajas-Morales (1987)
Euphorbia pseudograntii	0.329	0	Mens (2020)
	0.466	3	Benthall (1984)
Euphorbia spp.			Goldsmith & Carter (1981)
T 1. 1'. (' II'	0.476	0	Barajas-Morales (1987)
Euphorbia tirucalli	0.476	0	Mens (2020)
Faurea saligna	0.673	0	Mens (2020)
Fernandoa magnifica	0.63	3	Carsan et al. (2012)
Ficus faulkneriana	0.405	2	Carsan et al. (2012)
Ficus lutea	0.405	2	Carsan et al. (2012)
Ficus spp.	0.405	2	Carsan et al. (2012)
Ficus sur	0.46	0	Uganda Forest Department (1992)
Ficus sycomorus	0.413	0	Carsan et al. (2012)
Ficus vasta	0.405	2	Carsan et al. (2012)
Flacourtia indica	0.67	0	Mens (2020)
Fleroya rubrostipulata	0.537	0	Takahashi (1978)
Flueggea virosa	0.75	0	Mens (2020)
Garcinia livingstonei	0.732	0	Goldsmith & Carter (1981)
Gnidia latifolia	0.744	0	Mens (2020)
Grevillea spp.	0.63	3	Carsan et al. (2012)
Grewia bicolor	0.808	0	Mens (2020)
Grewia lilacina	0.585	3	Carsan et al. (2012)
Grewia plagiophylla	0.585	3	Carsan et al. (2012)
Grewia spp.	0.585	3	Carsan et al. (2012)
Grewia tristis	0.585	3	Carsan et al. (2012)
Gymnosporia buxifolia	0.694	0	Mens (2020)
Gymnosporia heterophylla	0.53	2	Carsan et al. (2012)
Harrisonia abyssinica	0.785	3	Carsan et al. (2012)
Harungana madagascariensis	0.4595	0	Carsan et al. (2012)
Heinsia crinita	0.65	4	Zanne et al. (2009)
Hibiscus spp.	0.477	3	Carsan et al. (2012)
Hippocratea spp.	0.87	3	Carsan et al. (2012)
Hoslundia opposita	0.46	4	Zanne et al. (2009)
Hyphaene compressa	0.54	5	Zanne et al. (2009)
Indigofera lupatana	0.65	4	Zanne et al. (2009)
Intropho ann	0.369	3	Correct et al. (2012)
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Jatropha spp.			Carsan et al. (2012)
Keetia spp.	0.65	4	Zanne et al. (2009)
Keetia venosa	0.65	4	Zanne et al. (2009)
Keetia zanzibarica	0.65	4	Zanne et al. (2009)
Lannea schweinfurthii	0.661	0	Mens (2020)
Lannea spp.	0.469	3	Carsan et al. (2012)
	0.437	0	Brown (1997)
Lannea welwitschii			Reyes et al. (1992)
			Uganda Forest Department (1992)
Lantana camara	0.484	0	Mens (2020)
Lantana spp.	0.52	2	Uganda Forest Department (1992)
Lawsonia inermis	0.58	5	Zanne et al. (2009)
Leucaena spp.	0.72	3	Carsan et al. (2012)
Lonchocarpus bussei	0.75	3	Carsan et al. (2012)
Lonchocarpus eriocalyx	0.75	3	Carsan et al. (2012)
Lonchocarpus spp.	0.75	3	Carsan et al. (2012)
Lonchocarpus violaceus	0.75	3	Carsan et al. (2012)
Mangifera indica	0.616	0	Mens (2020)
Margaritaria discoidea	0.727	0	Carsan et al. (2012)
Markhamia zanzibarica	0.775	0	Goldsmith & Carter (1981)
Mascarenhasia spp.	0.45	4	Zanne et al. (2009)
Maytenus buchananii	0.7	3	Carsan et al. (2012)
Melia spp.	0.485	3	Carsan et al. (2012)
Melia volkensii	0.671	0	Mens (2020)
Meyna tetraphylla	0.65	4	Zanne et al. (2009)
	0.55	0	Government of Ethiopia (2016)
Milicia excelsa			Carsan et al. (2012)
			Uganda Forest Department (1992)
Mimosa pigra	0.729	1	Carsan et al. (2012)
Momordica rostrata	NA	NA	NA
Ochna kirkii	0.8	3	Mens (2020)
Ochna mossambicensis	0.7515	3	Carsan et al. (2012)
Ochna spp.	0.7515	3	Carsan et al. (2012)
Ocimum gratissimum	0.46	4	Zanne et al. (2009)
Ocimum kilimandscharicum	0.46	4	Zanne et al. (2009)
Ocimum spp.	0.46	4	Zanne et al. (2009)
Oncoba spp.	0.65	3	Carsan et al. (2012)
Ormocarpum spp.	0.742	2	Goldsmith & Carter (1981)
Osyris lanceolata	0.854	3	Carsan et al. (2012)
Ouratea spp.	0.785	3	Carsan et al. (2012)

Ozoroa insignis	0.498	0	Mens (2020)
Pappea capensis	0.883	0	Goldsmith & Carter (1981)
Parinari curatellifolia	0.616	0	Mens (2020)
	0.5025	0	Carsan et al. (2012)
Parkia filicoidea			Uganda Forest Department (1992)
Pavetta lanceolata	0.65	4	Zanne et al. (2009)
Pentanisia ouranogyne	0.65	4	Zanne et al. (2009)
Phoenix reclinata	0.54	5	Zanne et al. (2009)
Phyllanthus spp.	0.6715	3	Carsan et al. (2012)
Plectranthus spp.	0.46	4	Zanne et al. (2009)
Polyscias fulva	0.385	0	Government of Ethiopia (2016) Carsan et al. (2012) Uganda Forest Department (1992)
Polyscias spp.	0.3698	3	Carsan et al. (2012)
Polysphaeria parvifolia	0.65	4	Zanne et al. (2009)
Premna chrysoclada	0.568	3	Carsan et al. (2012)
Premna spp.	0.568	3	Carsan et al. (2012)
Prunus spp.	0.5708	3	Carsan et al. (2012)
Psidium guajava	0.63	0	Uganda Forest Department (1992)
Psychotria fractinervata	0.52	3	Carsan et al. (2012)
Psychotria spp.	0.52	3	Carsan et al. (2012)
Rauvolfia mombasiana	0.4665	3	Carsan et al. (2012)
Rhus natalensis	0.542	3	Carsan et al. (2012)
Rhus spp.	0.542	3	Carsan et al. (2012)
Rotheca spp.	0.46	4	Zanne et al. (2009)
Rourea orientalis	0.71	3	Carsan et al. (2012)
Rytigynia spp.	0.65	4	Zanne et al. (2009)
Saba comorensis	0.45	4	Zanne et al. (2009)
Santalum album	0.9435	1	Carsan et al. (2012)
Sclerocarya birrea	0.603	0	Mens (2020)
Sclerocarya spp.	0.508	2	Carsan et al. (2012)
Scolopia spp.	0.794	3	Carsan et al. (2012)
Securidaca longipedunculata	0.765	0	Uganda Forest Department (1992)
Senna siamea	0.665	1	Carsan et al. (2012)
Senna singueana	0.664	0	Mens (2020)
Senna spectablis	0.433	0	Mens (2020)
Senna spp.	0.6035	3	Carsan et al. (2012)
Solanum incanum	0.44	3	Carsan et al. (2012)
Sorindeia madagascariensis	0.56	0	Munishi et al. (2004)
Spathodea campanulata	0.232	0	Carsan et al. (2012)

Sphaerocoryne spp.	0.7	4	Zanne et al. (2009)
<u> </u>	0.37	0	Government of Ethiopia (2016)
Steganotaenia araliacea			Uganda Forest Department (1992)
Steganotaenia spp.	0.37	2	Uganda Forest Department (1992)
	0.3855	0	Goldsmith & Carter (1981)
Sterculia africana			Vreugdenhil et al. (2012)
Sterculia spp.	0.47	3	Carsan et al. (2012)
Stereospermum kunthianum	0.6315	0	Goldsmith & Carter (1981)
	0.584	0	Goldsmith & Carter (1981)
Strombosia scheffleri			Munishi et al. (2004)
Strychnos madagascariensis	0.663	0	Goldsmith & Carter (1981)
	0.6695	0	Goldsmith & Carter (1981)
Strychnos spinosa			Nygård & Elfving (2000)
Styasasia spp.	0.66	4	Zanne et al. (2009)
Suregada zanzibariensis	0.6615	3	Carsan et al. (2012)
Company along have the	0.6775	2	Munishi et al. (2004)
Synsepalum brevipes			Sallenave (1955)
Sunsanalum dula:fiaum	0.6775	2	Munishi et al. (2004)
Synsepalum dulcificum			Sallenave (1955)
Synsepalum spp.	0.6775	2	Munishi et al. (2004)
Synsepatum spp.			Sallenave (1955)
	0.62	0	Goldsmith & Carter (1981)
Syzygium cordatum			Reyes et al. (1992)
			Uganda Forest Department (1992)
Tabernaemontana elegans	0.646	0	Goldsmith & Carter (1981)
Tamarindus indica	0.792	0	Mens (2020)
Teclea spp.	0.825	2	Goldsmith & Carter (1981)
Terea spp.			Uganda Forest Department (1992)
Tectona grandis	0.607	0	Carsan et al. (2012)
			Uganda Forest Department (1992)
Terminalia brownii	0.889	0	Mens (2020)
Tetracera boiviniana	0.63	5	Zanne et al. (2009)
Thespesia danis	0.65	3	Carsan et al. (2012)
F			Reyes et al. (1992)
Thespesia garckeana	0.687	0	Mens (2020)
Thevetia spp.	0.72	3	Barajas-Morales (1987)
Thevetia thevetioides	0.72	3	Barajas-Morales (1987)
Thunbergia spp.	0.66	5	Zanne et al. (2009)
Tinnea aethiopica	0.46	4	Zanne et al. (2009)
Trema orientalis	0.403	0	Reyes et al. (1992)
			Uganda Forest Department (1992)

T 1	0.5275	0	C
Trichilia emetica	0.5375	0	Carsan et al. (2012)
Turraea floribunda	0.663	2	Goldsmith & Carter (1981)
Turraea nilotica	0.663	0	Goldsmith & Carter (1981)
Turraea wakefieldii	0.663	2	Goldsmith & Carter (1981)
Uvaria acuminata	0.353	3	Carsan et al. (2012)
Uvaria lucida	0.852	0	Mens (2020)
Uvaria scheffleri	0.353	3	Carsan et al. (2012)
Vangueria infausta	0.689	0	Goldsmith & Carter (1981)
Vangueria madagascariensis	0.676	2	Goldsmith & Carter (1981)
Vangueria spp.	0.676	2	Goldsmith & Carter (1981)
Vernonia hymenolepis	0.37	3	Carsan et al. (2012)
Vernonia spp.	0.37	3	Carsan et al. (2012)
Vernonia zanzibarica	0.37	3	Carsan et al. (2012)
Vismia spp.	0.489	3	Carsan et al. (2012)
Vitex doniana	0.469	0	Carsan et al. (2012)
Vitex keniensis	0.625	0	Mens (2020)
Vitex mombassae	0.451	2	Carsan et al. (2012)
Vitex oxycuspis	0.499	0	Kryn & Fobes (1959)
Waltheria spp.	0.54	4	Zanne et al. (2009)
XX7. 1	0.832	0	Government of Ethiopia (2016)
Warburgia ugandanesis			Uganda Forest Department (1992)
Wrightia regina	0.55	3	Carsan et al. (2012)
Wrightia stuhlmannii	0.55	3	Carsan et al. (2012)
Xylopia parviflora	0.81	0	Monteiro et al. (1971)
Zanthoxylum chalybeum	0.64	3	Carsan et al. (2012)

Appendix Table 3. SLA values for all woody species across sites. Accuracy column reflects how specific the SLA values are for each species: l = species-specific; 2 = genus-specific; 3 = family-specific.

Species	Median SLA (mm ² mg ⁻¹)	Accuracy	Source
Acacia drepanolobium	7.903411927	1	Kattge et al. (2020)
Acacia hockii	7.903411927	1	Kattge et al. (2020)
Acacia mellifera	5.52	0	Kattge et al. (2020)
Acacia nilotica	10.40334834	0	Kattge et al. (2020)
Acacia nubica	7.903411927	1	Kattge et al. (2020)
Acacia senegal	13.05090653	0	Kattge et al. (2020)
Acacia seyal	7.903411927	1	Kattge et al. (2020)

· · · · · · · · · · · · · · · · · · ·	7.002411027	1	V. (1 1. (2020)
Acacia spp.	7.903411927	1	Kattge et al. (2020)
Acacia stuhlmannii	7.903411927	1	Kattge et al. (2020)
Acacia tortilis	10.21307529	0	Kattge et al. (2020)
Adansonia digitata	15	0	Kattge et al. (2020)
Afrocanthium spp.	18.05054152	2	Kattge et al. (2020)
Afzelia quanzensis	16.27547208	2	Kattge et al. (2020)
Albizia adianthifolia	10.4	0	Kattge et al. (2020)
Albizia anthelmintica	17.42695293	1	Kattge et al. (2020)
Albizia versicolor	17.42695293	1	Kattge et al. (2020)
Alchornea spp.	17.19121761	1	Kattge et al. (2020)
Allophylus rubifolius	22.79074457	1	Kattge et al. (2020)
Anacardium occidentale	11.51090593	0	Kattge et al. (2020)
Anisotes spp.	22.08401418	2	Kattge et al. (2020)
Anisotes ukambensis	22.0840142	2	Kattge et al. (2020)
Annona senegalensis	12.11141353	1	Kattge et al. (2020)
Annona spp.	12.11141353	1	Kattge et al. (2020)
Antidesma venosum	9.455225057	0	Kattge et al. (2020)
Apodytes dimidiata	7.012582906	0	Kattge et al. (2020)
Artocarpus heterophyllus	9.662993786	0	Kattge et al. (2020)
Aspilia spp.	16.94	2	Kattge et al. (2020)
Azadirachta indica	17.03486171	0	Kattge et al. (2020)
Balanites aegyptiaca	7.88	1	Kattge et al. (2020)
Barringtonia racemosa	13.24536813	1	Kattge et al. (2020)
Bauhinia acuminata	16.63800086	1	Kattge et al. (2020)
Bauhinia thonningii	16.63800086	1	Kattge et al. (2020)
Bixa spp.	16.98617776	1	Kattge et al. (2020)
Blighia unijugata	13	1	Kattge et al. (2020)
Borassus aethiopum	11.1067285	2	Kattge et al. (2020)
Boscia angustifolia	5.264451314	1	Kattge et al. (2020)
Boscia coriacea	5.264451314	1	Kattge et al. (2020)
Bourreria petiolaris	10.12811039	1	Kattge et al. (2020)
Bourreria spp.	10.12811039	1	Kattge et al. (2020)
Brachystegia spiciformis	8.495	0	Kattge et al. (2020)
Brackenridgea zanguebarica	11.7568	2	Kattge et al. (2020)
Bridelia cathartica	3.01	0	Kattge et al. (2020)
Bridelia micrantha	11.73392882	1	Kattge et al. (2020)
Bridelia spp.	11.73392882	1	Kattge et al. (2020)
Bridelia taitensis	11.73392882	1	Kattge et al. (2020)
Buddleja spp.	10.13481013	1	Kattge et al. (2020)
Buttonia spp.	20.27775451	2	Kattge et al. (2020)

Caesalpinia bonduc 24.54380294 1 Kattge et al. (2020) Calotropis procera 17.90679213 2 Kattge et al. (2020) Canthium spp. 13.78200992 1 Kattge et al. (2020) Capparis tomentosa 2.23 0 Kattge et al. (2020) Carica papaya 42.89363277 1 Kattge et al. (2020) Carissa edulis 12.17962177 0 Kattge et al. (2020) Cassia abbreviata 5.22 0 Kattge et al. (2020) Cassia afrofistula 19.98472589 1 Kattge et al. (2020) Cassipourca spp. 12.49721608 1 Kattge et al. (2020) Cassair aquisetifolia 2.773925104 0 Kattge et al. (2020) Catta edulis 12.83254559 2 Kattge et al. (2020) Chassalia umbraticola 18.05054152 2 Kattge et al. (2020) Citrus sinensis 10.58468997 0 Kattge et al. (2020) Citrus sinensis 10.58468997 0 Kattge et al. (2020) Cierodendrum spp. 28.03718293 1 Kat	
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Combretum collinum8.760Kattge et al. (2020)	
Combretum fragrans 15.12290739 1 Kattge et al. (2020)	
Combretum molle 10.93630572 0 Kattge et al. (2020)	
Combretum schumannii15.11014191Kattge et al. (2020)	
Combretum spp. 15.1101419 1 Kattge et al. (2020)	
Combretum zeyheri5.3650Kattge et al. (2020)	
Commiphora africana12.713454971Kattge et al. (2020)	
Commiphora spp. 12.71345497 1 Kattge et al. (2020)	
Cordia africana 15.55797594 1 Kattge et al. (2020)	
Cordia monoica 15.52928978 1 Kattge et al. (2020)	
Cremaspora spp. 18.05054152 2 Kattge et al. (2020)	
Crossopteryx febrifuga1.960Kattge et al. (2020)	
Crotalaria agatiflora 28.88828479 1 Kattge et al. (2020)	
Crotalaria spp. 28.88828479 1 Kattge et al. (2020)	
Croton dichogamus 18.63569207 1 Kattge et al. (2020)	
Croton megalocarpus 18.63569207 1 Kattge et al. (2020)	
Croton spp. 18.63569207 1 Kattge et al. (2020)	
Dalbergia boehmii 10.95904091 1 Kattge et al. (2020)	
Dalbergia melanoxylon7.809250Kattge et al. (2020)	
Deinbollia spp. 11.3 1 Kattge et al. (2020)	
Desmodium spp. 19.41389662 1 Kattge et al. (2020)	
Dichrostachys cinerea 12.17539705 0 Kattge et al. (2020)	
Diospyros abyssinica 11.8957424 1 Kattge et al. (2020)	

Diopyros squarrosa11.8974241Kattge et al. (2020)Dodonaea spp.7.6811127621Kattge et al. (2020)Dombeya burgessiae15.222965461Kattge et al. (2020)Dombeya nukole15.222965461Kattge et al. (2020)Dombeya spp.15.222965461Kattge et al. (2020)Dracaena spp.17.328428591Kattge et al. (2020)Ehretia spn.11.33064031Kattge et al. (2020)Ehretia spn.7.4328571430Kattge et al. (2020)Eythrija abyssinica26.536049451Kattge et al. (2020)Erythrophleum suaveolens16.275472082Kattge et al. (2020)Euclea spp.9.5359383751Kattge et al. (2020)Euclea spp.6.3692137511Kattge et al. (2020)Euphorbia bussei23.212155511Kattge et al. (2020)Euphorbia pseudogranti23.212155511Kattge et al. (2020)Euphorbia pseudogranti23.212155511Kattge et al. (2020)Fernadoa magnifica17.434620482Kattge et al. (2020)Ficus futa14.476922471Kattge et al. (2020)Ficus surt14.476922471Kattge et al. (2020)Ficus surt14.47				
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Dombeya burgessiae 15:2296546 1 Kattge et al. (2020) Dombeya mukole 15:22296546 1 Kattge et al. (2020) Dombeya spp. 15:22296546 1 Kattge et al. (2020) Dracaena spp. 17:28242859 1 Kattge et al. (2020) Ekretia spp. 11:306403 1 Kattge et al. (2020) Ekretia spp. 11:306403 1 Kattge et al. (2020) Ekretia spp. 11:306403 1 Kattge et al. (2020) Ergthrophicum suaveolens 16:27547208 2 Kattge et al. (2020) Eucalyptus spp. 9:535938375 1 Kattge et al. (2020) Eucalyptus spp. 2:321215551 1 Kattge et al. (2020) Eucalptus spp. 2:321215551 1 Kattge et al. (2020) Euphorbia bussei 2:321215551 1 Kattge et al. (2020) Eughorbia trucalli 2:321215551 1 Kattge et al. (2020) Fernandom magnifica 1:4:456247 1 Kattge et al. (2020) Ficus suc 1:4:4:692247 1 Kattge et al. (2020				
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Flueggea virosa 17.13642243 0 Kattge et al. (2020) Garcinia livingstonei 9.495527723 1 Kattge et al. (2020) Gnidia latifolia 17.77601458 2 Kattge et al. (2020) Grevillea spp. 6.599623096 1 Kattge et al. (2020) Grewia bicolor 18.28786024 0 Kattge et al. (2020) Grewia lilacina 16.32088054 1 Kattge et al. (2020) Grewia spp. 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Flacourtia indica	28.05	0	Kattge et al. (2020)
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Grewia bicolor 18.28786024 0 Kattge et al. (2020) Grewia lilacina 16.32088054 1 Kattge et al. (2020) Grewia plagiophylla 16.32088054 1 Kattge et al. (2020) Grewia spp. 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Gnidia latifolia	17.77601458	2	Kattge et al. (2020)
Grewia lilacina 16.32088054 1 Kattge et al. (2020) Grewia plagiophylla 16.32088054 1 Kattge et al. (2020) Grewia spp. 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Grevillea spp.	6.599623096	1	Kattge et al. (2020)
Grewia plagiophylla 16.32088054 1 Kattge et al. (2020) Grewia spp. 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Grewia bicolor	18.28786024	0	Kattge et al. (2020)
Grewia spp. 16.32088054 1 Kattge et al. (2020) Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Grewia lilacina	16.32088054	1	Kattge et al. (2020)
Grewia tristis 16.32088054 1 Kattge et al. (2020) Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Grewia plagiophylla	16.32088054	1	Kattge et al. (2020)
Gymnosporia buxifolia 10.63529596 0 Kattge et al. (2020) Gymnosporia heterophylla 9.013828025 1 Kattge et al. (2020)	Grewia spp.	16.32088054	1	Kattge et al. (2020)
Gymnosporia heterophylla9.0138280251Kattge et al. (2020)	Grewia tristis	16.32088054	1	Kattge et al. (2020)
Gymnosporia heterophylla9.0138280251Kattge et al. (2020)	Gymnosporia buxifolia	10.63529596	0	Kattge et al. (2020)
			1	
Harrisonia abyssinica 13.447 1 Kattge et al. (2020)	Harrisonia abyssinica		1	Kattge et al. (2020)

Homingono modogosoonionsis	10 92422702	0	Kattge et al. (2020)
Harungana madagascariensis	10.83423793	-	
Heinsia crinita	18.05054152	2	Kattge et al. (2020)
Hibiscus spp.	27.61194734	1	Kattge et al. (2020)
Hippocratea spp.	19.8163207	1	Kattge et al. (2020)
Hoslundia opposita	18.83239171	2	Kattge et al. (2020)
Hyphaene compressa	11.10672854	2	Kattge et al. (2020)
Indigofera lupatana	18.96108726	1	Kattge et al. (2020)
Jatropha curcas	16.79554261	1	Kattge et al. (2020)
Jatropha spp.	16.79554261	1	Kattge et al. (2020)
Keetia spp.	18.05054152	2	Kattge et al. (2020)
Keetia venosa	18.05054152	2	Kattge et al. (2020)
Keetia zanzibarica	18.05054152	2	Kattge et al. (2020)
Lannea schweinfurthii	4.837666667	0	Kattge et al. (2020)
Lannea spp.	10.05523321	1	Kattge et al. (2020)
Lannea welwitschii	10.05523321	1	Kattge et al. (2020)
Lantana camara	21.03449761	0	Kattge et al. (2020)
Lantana spp.	18.95223136	1	Kattge et al. (2020)
Lawsonia inermis	16.4959799	2	Kattge et al. (2020)
Leucaena spp.	16.54091687	1	Kattge et al. (2020)
Lonchocarpus bussei	16.47361212	1	Kattge et al. (2020)
Lonchocarpus eriocalyx	16.47361212	1	Kattge et al. (2020)
Lonchocarpus spp.	16.47361212	1	Kattge et al. (2020)
Lonchocarpus violaceus	16.47361212	1	Kattge et al. (2020)
Mangifera indica	8.162631859	0	Kattge et al. (2020)
Margaritaria discoidea	27.6102754	1	Kattge et al. (2020)
Markhamia zanzibarica	17.43462048	2	Kattge et al. (2020)
Mascarenhasia spp.	17.90679213	2	Kattge et al. (2020)
Maytenus buchananii	60.28030962	1	Kattge et al. (2020)
Melia spp.	13.95484824	1	Kattge et al. (2020)
Melia volkensii	13.95484824	1	Kattge et al. (2020)
Meyna tetraphylla	18.05054152	2	Kattge et al. (2020)
Milicia excelsa	35.33333333	0	Kattge et al. (2020)
Mimosa pigra	17.56648695	1	Kattge et al. (2020)
Momordica rostrata	17.7768616	2	Kattge et al. (2020)
Ochna kirkii	15.0060831	1	Kattge et al. (2020)
Ochna mossambicensis	15.0060831	1	Kattge et al. (2020)
Ochna spp.	15.0060831	1	Kattge et al. (2020)
Ocimum gratissimum	37.87878788	1	Kattge et al. (2020)
Ocimum kilimandscharicum	37.87878788	1	Kattge et al. (2020)
Ocimum spp.	37.87878788	1	Kattge et al. (2020)

Oncoba spp.	13.55814316	2	Kattge et al. (2020)
Ormocarpum spp.	13.44523952	1	Kattge et al. (2020)
Osyris lanceolata	8.75	1	Kattge et al. (2020)
Ouratea spp.	11.18882433	1	Kattge et al. (2020)
Ozoroa insignis	8.816611523	1	Kattge et al. (2020)
Pappea capensis	10.0644253	0	Kattge et al. (2020)
Parinari curatellifolia	10.05846476	1	Kattge et al. (2020)
Parkia filicoidea	14.51059056	1	Kattge et al. (2020)
Pavetta lanceolata	18.05054152	2	Kattge et al. (2020)
Pentanisia ouranogyne	18.05054152	2	Kattge et al. (2020)
Phoenix reclinata	5.188000459	1	Kattge et al. (2020)
Phyllanthus spp.	15.17203109	1	Kattge et al. (2020)
Plectranthus spp.	5.188000459	1	Kattge et al. (2020)
Polyscias fulva	23.01274864	1	Kattge et al. (2020)
Polyscias spp.	23.01274864	1	Kattge et al. (2020)
Polysphaeria parvifolia	18.05054152	2	Kattge et al. (2020)
Premna chrysoclada	31.83764586	1	Kattge et al. (2020)
Premna spp.	31.83764586	1	Kattge et al. (2020)
Prunus spp.	15.15341899	1	Kattge et al. (2020)
Psidium guajava	9.903251738	0	Kattge et al. (2020)
Psychotria fractinervata	21.24333241	1	Kattge et al. (2020)
Psychotria spp.	21.24333241	1	Kattge et al. (2020)
Rauvolfia mombasiana	35.24855564	1	Kattge et al. (2020)
Rhus natalensis	20.79228954	1	Kattge et al. (2020)
Rhus spp.	20.79228954	1	Kattge et al. (2020)
Rotheca spp.	18.83239171	2	Kattge et al. (2020)
Rourea orientalis	16.44552412	1	Kattge et al. (2020)
Rytigynia spp.	18.05054152	2	Kattge et al. (2020)
Saba comorensis	17.90679213	2	Kattge et al. (2020)
Santalum album	3.758010661	1	Kattge et al. (2020)
Sclerocarya birrea	10.03195419	0	Kattge et al. (2020)
Sclerocarya spp.	10.03195419	1	Kattge et al. (2020)
Scolopia spp.	9.546397393	1	Kattge et al. (2020)
Securidaca longipedunculata	14.80356019	1	Kattge et al. (2020)
Senna siamea	13.58463033	1	Kattge et al. (2020)
Senna singueana	13.58463033	1	Kattge et al. (2020)
Senna spectabilis	13.58463033	1	Kattge et al. (2020)
Senna spp.	13.58463033	1	Kattge et al. (2020)
Solanum incanum	137.9060335	1	Kattge et al. (2020)
Sorindeia madagascariensis	13.09	2	Kattge et al. (2020)

	25.0954	0	V. (1. (2020)
Spathodea campanulata	25.0854	0	Kattge et al. (2020)
Sphaerocoryne spp.	15.38542841	2	Kattge et al. (2020)
Steganotaenia araliacea	18.88016644	2	Kattge et al. (2020)
Steganotaenia spp.	18.88016644	2	Kattge et al. (2020)
Sterculia africana	14.36591963	1	Kattge et al. (2020)
Sterculia spp.	14.36591963	1	Kattge et al. (2020)
Stereospermum kunthianum	17.43462048	2	Kattge et al. (2020)
Strombosia scheffleri	9.381685432	1	Kattge et al. (2020)
Strychnos madagascariensis	8.028469166	0	Kattge et al. (2020)
Strychnos spinosa	17.31965288	0	Kattge et al. (2020)
Styasasia spp.	22.08401418	2	Kattge et al. (2020)
Suregada zanzibariensis	8.572948123	0	Kattge et al. (2020)
Synsepalum brevipes	10.5	2	Kattge et al. (2020)
Synsepalum dulcificum	10.5	2	Kattge et al. (2020)
Synsepalum spp.	10.5	2	Kattge et al. (2020)
Syzygium cordatum	9.581190231	1	Kattge et al. (2020)
Tabernaemontana elegans	17.90679213	2	Kattge et al. (2020)
Tamarindus indica	6.25	0	Kattge et al. (2020)
Teclea spp.	14.04333333	1	Kattge et al. (2020)
Tectona grandis	10.02585253	0	Kattge et al. (2020)
Terminalia brownii	17.12951379	1	Kattge et al. (2020)
Tetracera boiviniana	18.16743755	1	Kattge et al. (2020)
Thespesia danis	14.84754763	1	Kattge et al. (2020)
Thespesia garckeana	14.84754763	1	Kattge et al. (2020)
Thevetia spp.	19.90858078	1	Kattge et al. (2020)
Thevetia thevetioides	19.90858078	1	Kattge et al. (2020)
Thunbergia spp.	22.08401418	2	Kattge et al. (2020)
Tinnea aethiopica	18.83239171	2	Kattge et al. (2020)
Trema orientalis	12.99028791	0	Kattge et al. (2020)
Trichilia emetica	16.69468038	1	Kattge et al. (2020)
Turraea floribunda	15.68092092	2	Kattge et al. (2020)
Turraea nilotica	15.68092092	2	Kattge et al. (2020)
Turraea wakefieldii	15.68092092	2	Kattge et al. (2020)
Uvaria acuminata	11.58625	1	Kattge et al. (2020)
Uvaria lucida	11.58625	1	Kattge et al. (2020)
Uvaria scheffleri	11.58625	1	Kattge et al. (2020)
Vangueria infausta	18.05054152	2	Kattge et al. (2020)
Vangueria madagascariensis	18.05054152	2	Kattge et al. (2020)
Vangueria spp.	18.05054152	2	Kattge et al. (2020)
Vernonia hymenolepis	24.97700063	1	Kattge et al. (2020)

Vernonia spp.	24.97700063	1	Kattge et al. (2020)
Vernonia zanzibarica	24.97700063	1	Kattge et al. (2020)
Vismia spp.	14.83491706	1	Kattge et al. (2020)
Vitex doniana	19.61443121	1	Kattge et al. (2020)
Vitex keniensis	19.61443121	1	Kattge et al. (2020)
Vitex mombassae	19.61443121	1	Kattge et al. (2020)
Vitex oxycuspis	19.61443121	1	Kattge et al. (2020)
Waltheria spp.	10.35707605	1	Kattge et al. (2020)
Warburgia ugandensis	7.762636308	2	Kattge et al. (2020)
Wrightia regina	18.04357725	1	Kattge et al. (2020)
Wrightia stuhlmannii	18.04357725	1	Kattge et al. (2020)
Xylopia parviflora	13.41811186	1	Kattge et al. (2020)
Zanthoxylum chalybeum	15.14235631	1	Kattge et al. (2020)

Appendix Table 4. Deciduousness values for all woody species across sites. Deciduousness values reflect different functional strategies of woody species: 0 = evergreen; 0.5 = semi-deciduous; 1 = deciduous. NA is given when no deciduousness value was available. Accuracy reflects how specific the deciduousness values are for each species: 0 = species-specific; 1 = genus-specific. If a source is listed as Assumption no reliable academic source was available, instead the functional strategy is based on the functional strategy of other species in the same genus from the dataset.

Species	Deciduousness	Accuracy	Source
Acacia drepanolobium	0	1	Assumption
Acacia hockii	0	0	Fern (2019)
Acacia mellifera	0	1	Assumption
Acacia nilotica	0	0	Orwa et al. (2009)
Acacia nubica	0	1	Assumption
Acacia senegal	1	0	Kassa Merine et al. (2015)
Acacia seyal	1	0	Kassa Merine et al. (2015)
Acacia spp.	0	1	Assumption
Acacia stuhlmannii	0	1	Assumption
Acacia tortilis	0	0	Fern (2019)
Adansonia digitata	1	0	Maundu & Tengnäs (2005)
Afrocanthium spp.	NA	NA	NA
Afzelia quanzensis	0.5	0	Maundu & Tengnäs (2005)
Albizia adianthifolia	0	0	Kattge et al. (2020)
Albizia anthelmintica	1	0	Maundu & Tengnäs (2005)
Albizia versicolor	1	0	Fern (2019)
Alchornea spp.	0	1	Fern (2019)
Allophylus rubifolius	1	0	Mies & Beyl (1998)
Anacardium occidentale	0	0	Kattge et al. (2009)
Anisotes spp.	NA	NA	NA

Anisotes ukambensis	NA	NA	NA
Annona senegalensis	1	0	Fern (2019)
Annona spp.	1	1	Fern (2019)
Antidesma venosum	1	0	Fern (2019)
Apodytes dimidiata	0	0	Maundu & Tengnäs (2005)
Artocarpus heterophyllus	0	0	Wright et al. (2004)
Aspilia spp.	0	1	Assumption
Azadirachta indica	0	0	Maundu & Tengnäs (2005)
Balanites aegyptiaca	0	0	Maundu & Tengnäs (2005)
Barringtonia racemosa	0	0	Iversen et al. (2017)
Bauhinia acuminata	1	1	Chen et al. (2011)
Bauhinia thoningii	0	0	Chen et al. (2011)
Bixa spp.	0	1	Fern (2019)
Blighia unijugata	0	0	Sonibare et al. (2011)
Borassus aethiopum	0	0	Fern (2019)
Boscia angustifolia	0	0	Fern (2019)
Boscia coriacea	0	0	Maundu & Tengnäs (2005)
Bourreria petiolaris	0	1	Fern (2019)
Bourreria spp.	0	1	Fern (2019)
Brachystegia spiciformis	1	0	Maundu & Tengnäs (2005)
Brackenridgea zanguebarica	1	0	Tshisikhawe & Rooyen (2012)
Bridelia cathartica	0	0	Maroyi (2018)
Bridelia micrantha	0	0	Maundu & Tengnäs (2005)
Bridelia spp.	0	1	Maundu & Tengnäs (2005)
Bridelia taitensis	0	0	Mens (2020)
Buddleja spp.	0	1	Fern (2019)
Buttonia spp.	1	1	Ghazanfar et al. (2008)
Caesalpinia bonduc	1	1	Assumption
Calotropis procera	0	0	Frosi et al. (2012)
Canthium spp.	1	0	Lantz & Bremer (2004)
Capparis tomentosa	1	0	Fern (2019)
Carica papaya	0	0	Fern (2019)
Carissa edulis	0	0	Katende et al. (1995)
Cassia abbreviata	1	0	Maundu & Tengnäs (2005)
Cassia afrofistula	1	1	Fern (2019)
Cassia spp.	1	1	Fern (2019)
Cassipourea spp.	0	1	Assumption
Casuarina equisetifolia	1	0	Maundu & Tengnäs (2005)
Catha edulis	0	0	Mens (2020)
Chassalia umbraticola	0	0	Hyde et al. (2021)

Citrus limon	0	0	Kattge et al. (2020)
Citrus sinensis	0	0	Kattge et al. (2020)
Clerodendrum spp.	0	1	Maundu & Tengnäs (2005)
Cocos nucifera	0	0	Iversen et al. (2017)
Combretum collinum	0	0	Iversen et al. (2017)
Combretum fragrans	1	0	Fern (2019)
Combretum molle	0	0	Maundu & Tengnäs (2005)
Combretum schumannii	1	0	Fern (2019)
Combretum spp.	1	1	Maundu & Tengnäs (2005)
Combretum zeyheri	0	0	Iversen et al. (2017)
Commiphora africana	1	0	Maundu & Tengnäs (2005)
Commiphora spp.	1	1	Maundu & Tengnäs (2005)
Cordia africana	1	0	Maundu & Tengnäs (2005)
Cordia monoica	0	0	Fern (2019)
Cremaspora spp.	0	0	Meguro et al. (2018)
Crossopteryx febrifuga	1	0	Kattge et al. (2020)
Crotalaria agatiflora	0	0	Polhill (1982)
Crotalaria spp.	0	1	Polhill (1982)
Croton dichogamus	0.5	0	Mens (2020)
Croton megalocarpus	1	0	Maundu & Tengnäs (2005)
Croton spp.	1	1	Maundu & Tengnäs (2005)
Dalbergia boehmii	1	0	Hyde et al. (2021)
Dalbergia melanoxylon	1	0	Fern (2019)
Deinbollia spp.	0	1	Fern (2019)
Desmodium spp.	NA	NA	NA
Dichrostachys cinerea	1	0	Fern (2019)
Diospyros abyssinica	0	0	Maundu & Tengnäs (2005)
Diospyros cornii	0	0	Beentje (1994)
Diospyros squarrosa	1	0	Fern (2019)
Dodonaea spp.	0	1	Maundu & Tengnäs (2005)
Dombeya burgessiae	0.5	1	Assumption
Dombeya mukole	0	0	Kattge et al. (2020)
Dombeya spp.	1	1	Maundu & Tengnäs (2005)
Dracaena spp.	0	1	Maundu & Tengnäs (2005)
Ehretia spp.	1	1	Maundu & Tengnäs (2005)
Ekebergia capensis	0.5	0	Maundu & Tengnäs (2005)
Elaeis guineensis	0	0	Iversen et al. (2017)
Erythrina abyssinica	1	0	Maundu & Tengnäs (2005)
Erythrophleum suaveolens	0.5	0	Fern (2019)
Eucalyptus spp.	0	1	Maundu & Tengnäs (2005)
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Euglee ann	0	1	Maundu & Tananäa (2005)
Euclea spp.		1	Maundu & Tengnäs (2005)
Euphorbia bussei	0	0	Fern (2019)
Euphorbia pseudograntii	1	0	Mens (2020)
Euphorbia spp.	1	1	Mens (2020)
Euphorbia tirucalli	1	0	Mens (2020)
Faurea saligna	1	0	Maundu & Tengnäs (2005)
Fernandoa magnifica	1	0	Willan (1961)
Ficus faulkneriana	0	1	Halevy (1989)
Ficus lutea	1	1	Halevy (1989)
Ficus spp.	0	1	Halevy (1989)
Ficus sur	1	0	Maundu & Tengnäs (2005)
Ficus sycomorus	0.5	0	Maundu & Tengnäs (2005)
Ficus vasta	1	0	Negash (2010)
Flacourtia indica	1	0	Maundu & Tengnäs (2005)
Fleroya rubrostipulata	0	1	Assumption
Flueggea virosa	1	0	Maundu & Tengnäs (2005)
Garcinia livingstonei	0	0	Maundu & Tengnäs (2005)
Gnidia latifolia	0	0	Mens (2020)
Grevillea spp.	0.5	1	Maundu & Tengnäs (2005)
Grewia bicolor	1	0	Maundu & Tengnäs (2005)
Grewia lilacina	1	1	Maundu & Tengnäs (2005)
Grewia plagiophylla	1	1	Maundu & Tengnäs (2005)
Grewia spp.	1	1	Maundu & Tengnäs (2005)
Grewia tristis	1	1	Maundu & Tengnäs (2005)
Gymnosporia buxifolia	0	0	Mens (2020)
Gymnosporia heterophylla	1	0	da Silva et al. (2011)
Harrisonia abyssinica	0	0	Maundu & Tengnäs (2005)
Harungana madagascariensis	0	0	Fern (2019)
Heinsia crinita	0	0	Dawodu et al. (2019)
Hibiscus spp.	NA	NA	NA
Hippocratea spp.	NA	NA	NA
Hoslundia opposita	0	0	Hyde et al. (2021)
Hyphaene compressa	0	0	Fern (2019)
Indigofera lupatana	1	0	Njeru (2010)
Jatropha curcas	0.5	0	Fern (2019)
Jatropha spp.	0.5	1	Fern (2019)
Keetia spp.	0	0	Bridson (1986)
Keetia venosa	0	0	Bridson (1986)
Keetia zanzibarica	0	0	Bridson (1986)
Lannea schweinfurthii	1	0	Maundu & Tengnäs (2005)

Lannea spp.	1	1	Maundu & Tengnäs (2005)
Lannea welwitschii	0.5	0	Fern (2019)
Lantana camara	0	0	Kattge et al. (2020)
Lantana spp.	0	1	Fern (2019)
Lawsonia inermis	0	0	Fern (2019)
Leucaena spp.	0	1	Maundu & Tengnäs (2005)
Lonchocarpus bussei	1	0	Hyde et al. (2021)
Lonchocarpus eriocalyx	1	0	Manguro et al. (2018)
Lonchocarpus spp.	1	1	Hyde et al. (2021)
Lonchocarpus violaceus	0	0	Grandtner (2005)
Mangifera indica	0	0	Maundu & Tengnäs (2005)
Margaritaria discoidea	1	0	Maundu & Tengnäs (2005)
Markhamia zanzibarica	0	0	Fern (2019)
Mascarenhasia spp.	NA	NA	NA
Maytenus buchananii	0	0	Tebou et al. (2017)
Melia spp.	1	1	Maundu & Tengnäs (2005)
Melia volkensii	1	0	Fern (2019)
Meyna tetraphylla	1	1	Fern (2019)
Milicia excelsa	1	0	Fern (2019)
Mimosa pigra	0	0	Kattge et al. (2020)
Momordica rostrata	1	0	Fern (2019)
Ochna kirkii	0	0	Bandi et al. (2012)
Ochna mossambicensis	0	0	Bandi et al. (2012)
Ochna spp.	0	0	Bandi et al. (2012)
Ocimum gratissimum	1	0	Ryding (2000)
Ocimum kilimandscharicum	1	0	Paton (1992)
Ocimum spp.	1	1	Assumption
Oncoba spp.	0.5	1	Maundu & Tengnäs (2005)
Ormocarpum spp.	0	1	Maundu & Tengnäs (2005)
Osyris lanceolata	0	0	Maundu & Tengnäs (2005)
Ouratea spp.	NA	NA	NA
Ozoroa insignis	0.5	0	Maundu & Tengnäs (2005)
Pappea capensis	0.5	0	Maundu & Tengnäs (2005)
Parinari curatellifolia	0	0	Iversen et al. (2017)
Parkia filicoidea	1	0	Maundu & Tengnäs (2005)
Pavetta lanceolata	0	0	Fern (2019)
Pentanisia ouranogyne	1	1	Maroyi (2019)
Phoenix reclinata	0	0	Fern (2019)
Phyllanthus spp.	1	1	Fern (2019)
Plectranthus spp.	0	1	Fern (2019)

	1	0	
Polyscias fulva	1	0	Maundu & Tengnäs (2005)
Polyscias spp.	1	1	Maundu & Tengnäs (2005)
Polysphaeria parvifolia	0	0	Fern (2019)
Premna chrysoclada	0	1	Fern (2019)
Premna spp.	0	1	Fern (2019)
Prunus spp.	0	1	Maundu & Tengnäs (2005)
Psidium guajava	0	0	Maundu & Tengnäs (2005)
Psychotria fractinervata	1	0	Razafimandimbison (2014)
Psychotria spp.	1	1	Razafimandimbison (2014)
Rauvolfia mombasiana	0	0	Mukherjee et al. (2019)
Rhus natalensis	0	0	Jeruto et al. (2008)
Rhus spp.	0	1	Maundu & Tengnäs (2005)
Rotheca spp.	0	1	Mire (2016)
Rourea orientalis	1	0	Fern (2019)
Rytigynia spp.	1	1	Hyde et al. (2021)
Saba comorensis	NA	NA	NA
Santalum album	0	0	Lu et al. (2013)
Sclerocarya birrea	1	0	Maundu & Tengnäs (2005)
Sclerocarya spp.	1	1	Maundu & Tengnäs (2005)
Scolopia spp.	0	1	Fern (2019)
Securidaca longipedunculata	0	0	Fan et al. (2017)
Senna siamea	0	0	Maundu & Tengnäs (2005)
Senna singueana	1	0	Maundu & Tengnäs (2005)
Senna spectablis	1	0	Maundu & Tengnäs (2005)
Senna spp.	1	1	Maundu & Tengnäs (2005)
Solanum incanum	0	1	Fukuhara & Kubo (1991)
Sorindeia madagascariensis	0	0	Maundu & Tengnäs (2005)
Spathodea campanulata	1	0	Maundu & Tengnäs (2005)
Sphaerocoryne spp.	0	1	Hyde et al. (2021)
Steganotaenia araliacea	1	0	Fan et al. (2017)
Steganotaenia spp.	1	1	Fan et al. (2017)
Sterculia africana	1	0	Maundu & Tengnäs (2005)
Sterculia spp.	1	1	Maundu & Tengnäs (2005)
Stereospermum kunthianum	1	0	Maundu & Tengnäs (2005)
Strombosia scheffleri	0	0	Maundu & Tengnäs (2005)
Strychnos madagascariensis	1	0	Fern (2019)
Strychnos spinosa	0.5	0	Maundu & Tengnäs (2005)
Styasasia spp.	NA	NA	NA
Suregada zanzibariensis	0	0	Wright et al. (2004)
Synsepalum brevipes	0	0	Fern (2019)
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Synsepalum dulcificum	0	0	Fern (2019)
Synsepalum spp.	0	1	Fern (2019)
Syzygium cordatum	0	0	Maundu & Tengnäs (2005)
Tabernaemontana elegans	1	0	Jordaan (1979)
Tamarindus indica	0	0	Mens (2020)
	0	1	Orwa et al. (2009)
Teclea spp. Tectona grandis		0	
	1		Iversen et al. (2017)
Terminalia brownii	0.5	0	Maundu & Tengnäs (2005)
Tetracera boiviniana	0	1	Fern (2019)
Thespesia danis	1	0	Fern (2019)
Thespesia garckeana	0.5	0	Maundu & Tengnäs (2005)
Thevetia spp.	0	1	Hyde et al. (2021)
Thevetia thevetioides	0	0	Hyde et al. (2021)
Thunbergia spp.	0	0	Leahy (1992)
Tinnea aethiopica	NA	NA	NA
Trema orientalis	0	0	Kattge et al. (2020)
Trichilia emetica	0	0	Maundu & Tengnäs (2005)
Turraea floribunda	1	0	Roux (2003)
Turraea nilotica	1	0	Hyde et al. (2021)
Turraea wakefieldii	0	0	Beentje (1994)
Uvaria acuminata	0	1	Fern (2019)
Uvaria lucida	0.5	0	Mens (2020)
Uvaria scheffleri	0	1	Fern (2019)
Vangueria infausta	1	0	Maundu & Tengnäs (2005)
Vangueria madagascariensis	1	0	Maundu & Tengnäs (2005)
Vangueria spp.	1	1	Maundu & Tengnäs (2005)
Vernonia hymenolepis	0	1	Fern (2019)
Vernonia spp.	0	1	Habtemariam & Kereta (2020)
Vernonia zanzibarica	0	0	Hyde et al. (2021)
Vismia spp.	1	1	Bidgood (1992)
Vitex doniana	0.5	0	Maundu & Tengnäs (2005)
Vitex keniensis	1	0	Maundu & Tengnäs (2005)
Vitex mombassae	1	0	Maundu & Tengnäs (2005)
Vitex oxycuspis	1	0	Fern (2019)
Waltheria spp.	1	1	Verdoorn (1981)
Warburgia ugandanesis	0	0	Maundu & Tengnäs (2005)
Wrightia regina	0	1	Fern (2019)
Wrightia stuhlmannii	0	1	Fern (2019)
Xylopia parviflora	1	0	Verdcourt (1971)
Zanthoxylum chalybeum	1	0	Maundu & Tengnäs (2005)

Appendix Table 5. Nitrogen fixation values for all woody species across sites. Nitrogen fixation values reflect nitrogen-fixing capacity of species: 0 = no; 1 = yes. Species in Leguminosae are assumed to be nitrogen-fixing unless otherwise stated. If a source is listed as Assumption no reliable source was available and a value was assumed based on species taxonomic information.

Species	Nitrogen	Source
	Fixation	
Acacia drepanolobium	1	Leguminosae
Acacia hockii	1	Leguminosae
Acacia mellifera	1	Leguminosae
Acacia nilotica	1	Leguminosae
Acacia nubica	1	Leguminosae
Acacia senegal	1	Leguminosae
Acacia seyal	1	Leguminosae
Acacia spp.	1	Leguminosae
Acacia stuhlmannii	1	Leguminosae
Acacia tortilis	1	Leguminosae
Adansonia digitata	0	Werner et al. (2018)
Afrocanthium spp.	0	Assumption
Afzelia quanzensis	1	Leguminosae
Albizia adianthifolia	1	Leguminosae
Albizia anthelmintica	1	Leguminosae
Albizia versicolor	1	Leguminosae
Alchornea spp.	0	Assumption
Allophylus rubifolius	0	Assumption
Anacardium occidentale	0	Craine et al. (2009)
Anisotes spp.	0	Assumption
Anisotes ukambensis	0	Assumption
Annona senegalensis	0	Assumption
Annona spp.	0	Assumption
Antidesma venosum	0	Assumption
Apodytes dimidiata	0	Wright et al. (2004)
Artocarpus heterophyllus	0	Wright et al. (2004)
Aspilia spp.	0	Assumption
Azadirachta indica	0	Werner et al. (2014)
Balanites aegyptiaca	1	Hines & Eckman (1993)
Barringtonia racemosa	0	Werner et al. (2018)
Bauhinia acuminata	1	Leguminosae

Bauhinia thonningii	0	Werner et al. (2018)
Bixa spp.	0	Assumption
Blighia unijugata	0	Assumption
Borassus aethiopum	0	Assumption
Boscia angustifolia	0	Werner et al. (2018)
Boscia coriacea	0	Assumption
Bourreria petiolaris	0	Assumption
Bourreria spp.	0	Assumption
Brachystegia spiciformis	1	Leguminosae
Brackenridgea zanguebarica	0	Assumption
Bridelia cathartica	0	Assumption
Bridelia micrantha	0	Assumption
Bridelia spp.	0	Assumption
Bridelia taitensis	0	Mens (2020)
Buddleja spp.	0	Assumption
Buttonia spp.	0	Assumption
Caesalpinia bonduc	1	Leguminosae
Calotropis procera	0	Assumption
Canthium spp.	0	Assumption
Capparis tomentosa	0	Assumption
Carica papaya	0	Kattge et al. (2009)
Carissa edulis	0	Assumption
Cassia abbreviata	1	Leguminosae
Cassia afrofistula	1	Leguminosae
Cassia spp.	1	Leguminosae
Cassipourea spp.	0	Assumption
Casuarina equisetifolia	1	Assumption
Catha edulis	0	Mens (2020)
Chassalia umbraticola	0	Assumption
Citrus limon	0	Werner et al. (2014)
Citrus sinensis	0	Kattge et al. (2009)
Clerodendrum spp.	0	Assumption
Cocos nucifera	0	Werner et al. (2018)
Combretum collinum	0	Werner et al. (2014)
Combretum fragrans	0	Assumption
Combretum molle	0	Craine et al. (2009)
Combretum schumannii	0	Assumption
Combretum spp.	0	Assumption
Combretum zeyheri	0	Craine et al. (2009)
Commiphora africana	0	Werner et al. (2018)

Commiphora spp.	0	Assumption
Cordia africana	0	Assumption
Cordia monoica	0	Assumption
Cremaspora spp.	0	Assumption
Crossopteryx febrifuga	0	Assumption
Crotalaria agatiflora	1	Leguminosae
Crotalaria spp.	1	Leguminosae
Croton dichogamus	0	Mens 2020
Croton megalocarpus	1	IRENA (2019)
Croton spp.	0	Assumption
Dalbergia boehmii	1	Werner et al. (2014)
Dalbergia melanoxylon	1	Craine et al. (2009)
Deinbollia spp.	1	Leguminosae
Desmodium spp.	1	Leguminosae
Dichrostachys cinerea	1	Leguminosae
Diospyros abyssinica	0	Mens (2020)
Diospyros cornii	0	Mens (2020)
Diospyros squarrosa	0	Mens (2020)
Dodonaea spp.	0	Assumption
Dombeya burgessiae	0	Assumption
Dombeya mukole	0	Werner et al. (2014)
Dombeya spp.	0	Assumption
Dracaena spp.	0	Assumption
Ehretia spp.	0	Assumption
Ekebergia capensis	0	Wright et al. (2004)
Elaeis guineensis	0	Assumption
Erythrina abyssinica	1	Werner et al. (2014)
Erythrophleum suaveolens	1	Werner et al. (2014)
Eucalyptus spp.	0	Assumption
Euclea spp.	0	Assumption
Euphorbia bussei	0	Assumption
Euphorbia pseudograntii	0	Mens (2020)
Euphorbia spp.	0	Mens (2020)
Euphorbia tirucalli	0	Craine et al. (2009)
Faurea saligna	0	Werner et al. (2018)
Fernandoa magnifica	0	Assumption
Ficus faulkneriana	0	Assumption
Ficus lutea	0	Assumption
Ficus spp.	0	Assumption
Ficus sur	0	Assumption

Ficus sycomorus	1	Zewdie & Tadele (2015)
Ficus vasta	0	Assumption
Flacourtia indica	0	Mens (2020)
Fleroya rubrostipulata	0	Assumption
Flueggea virosa	0	Werner et al. (2014)
Garcinia livingstonei	0	Assumption
Gnidia latifolia	0	Mens (2020)
Grevillea spp.	0	Assumption
Grewia bicolor	0	Craine et al. (2009)
Grewia lilacina	0	Assumption
Grewia plagiophylla	0	Assumption
Grewia spp.	0	Assumption
Grewia tristis	0	Assumption
Gymnosporia buxifolia	0	Mens (2020)
Gymnosporia heterophylla	0	Assumption
Harrisonia abyssinica	0	Assumption
Harungana madagascariensis	0	Assumption
Heinsia crinita	0	Assumption
Hibiscus spp.	0	Assumption
Hippocratea spp.	0	Assumption
Hoslundia opposita	0	Assumption
Hyphaene compressa	0	Assumption
Indigofera lupatana	1	Werner et al. (2014)
Jatropha curcas	1	Madhaiyan et al. (2015)
Jatropha spp.	0	Assumption
Keetia spp.	0	Assumption
Keetia venosa	0	Assumption
Keetia zanzibarica	0	Assumption
Lannea schweinfurthii	0	Werner et al. (2018)
Lannea spp.	0	Assumption
Lannea welwitschii	0	Assumption
Lantana camara	0	Mens (2020)
Lantana spp.	0	Assumption
Lawsonia inermis	0	Assumption
Leucaena spp.	1	Maundu & Tengnäs (2005)
Lonchocarpus bussei	1	Werner et al. (2014)
Lonchocarpus eriocalyx	1	Werner et al. (2014)
Lonchocarpus spp.	1	Leguminosae
Lonchocarpus violaceus	1	Kattge et al. (2020)
Mangifera indica	0	Kattge et al. (2009)

Margaritaria discoidea	0	Assumption
Markhamia zanzibarica	0	Assumption
Mascarenhasia spp.	0	Assumption
Maytenus buchananii	0	Assumption
Melia spp.	0	Assumption
Melia volkensii	0	Mens (2020)
Meyna tetraphylla	0	Assumption
Milicia excelsa	0	Werner et al. (2018)
Mimosa pigra	1	Werner et al. (2014)
Momordica rostrata	0	Assumption
Ochna kirkii	0	Mens (2020)
Ochna mossambicensis	0	Assumption
Ochna spp.	0	Assumption
Ocimum gratissimum	0	Assumption
Ocimum kilimandscharicum	0	Assumption
Ocimum spp.	0	Assumption
Oncoba spp.	0	Assumption
Ormocarpum spp.	1	Leguminosae
Osyris lanceolata	0	Assumption
Ouratea spp.	0	Assumption
Ozoroa insignis	0	Mens (2020)
Pappea capensis	0	Kattge et al. (2020)
Parinari curatellifolia	0	Craine et al. (2009)
Parkia filicoidea	1	Werner et al. (2014)
Pavetta lanceolata	0	Assumption
Pentanisia ouranogyne	0	Assumption
Phoenix reclinata	0	Assumption
Phyllanthus spp.	0	Assumption
Plectranthus spp.	0	Assumption
Polyscias fulva	0	Assumption
Polyscias spp.	0	Assumption
Polysphaeria parvifolia	0	Assumption
Premna chrysoclada	0	Assumption
Premna spp.	0	Assumption
Prunus spp.	0	Assumption
Psidium guajava	0	Craine et al. (2009)
Psychotria fractinervata	0	Assumption
Psychotria spp.	0	Assumption
Rauvolfia mombasiana	0	Assumption
Rhus natalensis	0	Assumption

Rhus spp.	0	Assumption
Rotheca spp.	0	Assumption
Rourea orientalis	0	Assumption
Rytigynia spp.	0	Assumption
Saba comorensis	0	Assumption
Santalum album	0	Assumption
Sclerocarya birrea	0	Werner et al. (2014)
Sclerocarya spp.	0	Assumption
Scolopia spp.	0	Assumption
Securidaca longipedunculata	0	Assumption
Senna siamea	1	Werner et al. (2018)
Senna singueana	0	Mens (2020)
Senna spectabilis	0	Mens (2020)
Senna spp.	1	Leguminosae
Solanum incanum	0	Assumption
Sorindeia madagascariensis	0	Assumption
Spathodea campanulata	0	Werner et al. (2014)
Sphaerocoryne spp.	0	Assumption
Steganotaenia araliacea	0	Assumption
Steganotaenia spp.	0	Assumption
Sterculia africana	0	Assumption
Sterculia spp.	0	Assumption
Stereospermum kunthianum	0	Assumption
Strombosia scheffleri	0	Wright et al. (2004)
Strychnos madagascariensis	0	Werner et al. (2014)
Strychnos spinosa	0	Assumption
Styasasia spp.	0	Assumption
Suregada zanzibariensis	0	Wright et al. (2004)
Synsepalum brevipes	0	Assumption
Synsepalum dulcificum	0	Assumption
Synsepalum spp.	0	Assumption
Syzygium cordatum	0	Assumption
Tabernaemontana elegans	0	Assumption
Tamarindus indica	0	Craine et al. (2009)
Teclea spp.	0	Assumption
Tectona grandis	0	Craine et al. (2009)
Terminalia brownii	0	Mens (2020)
Tetracera boiviniana	0	Assumption
Thespesia danis	0	Assumption
Thespesia garckeana	0	Mens (2020)

Thevetia spp.	0	Assumption
Thevetia thevetioides	0	Assumption
Thunbergia spp.	0	Assumption
Tinnea aethiopica	0	Assumption
Trema orientalis	0	Werner et al. (2018)
Trichilia emetica	0	Assumption
Turraea floribunda	0	Assumption
Turraea nilotica	0	Assumption
Turraea wakefieldii	0	Assumption
Uvaria acuminata	0	Assumption
Uvaria lucida	0	Mens (2020)
Uvaria scheffleri	0	Assumption
Vangueria infausta	0	Craine et al. (2009)
Vangueria madagascariensis	0	Assumption
Vangueria spp.	0	Assumption
Vernonia hymenolepis	0	Assumption
Vernonia spp.	0	Assumption
Vernonia zanzibarica	0	Assumption
Vismia spp.	0	Assumption
Vitex doniana	1	Orwa et al. (2009)
Vitex keniensis	0	Mens (2020)
Vitex mombassae	0	Guo et al. (2017)
Vitex oxycuspis	0	Guo et al. (2017)
Waltheria spp.	0	Assumption
Warburgia ugandensis	0	Assumption
Wrightia regina	0	Assumption
Wrightia stuhlmannii	0	Assumption
Xylopia parviflora	0	Assumption
Zanthoxylum chalybeum	0	Assumption

SENASTE UTGIVNA NUMMER

2019:8	Författare: Hilda Mikaelsson Alternative oxidase respiration in the mycorrhizal fungus <i>Laccaria bicolor</i>
2019:9	Författare: Joel Jensen Above- and belowground carbon stocks and effects of enrichment planting in a tropical secondary lowland dipterocarp rainforest
2019:10	Författare: Josefin Runesson Total carbon sequestration during an entire rotation period of oil palm in northern Borneo
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