

## RESEARCH ARTICLE

## Towards effectively restoring agricultural landscapes in East African drylands: Linking plant functional traits with soil hydrology

Lotte Patty Mens<sup>1</sup>  | Aida Bargués-Tobella<sup>2</sup>  | Frank Sterck<sup>1</sup>  | Tor-Gunnar Vågen<sup>3</sup>  | Leigh Ann Winowiecki<sup>3</sup>  | Madelon Lohbeck<sup>1,3</sup> <sup>1</sup>Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, The Netherlands<sup>2</sup>Department of Forest Ecology and Management, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden<sup>3</sup>World Agroforestry (ICRAF), Nairobi, Kenya

## Correspondence

Lotte Patty Mens

Email: [lotte.mens88@gmail.com](mailto:lotte.mens88@gmail.com)

## Funding information

FONA Foundation for Research on Nature Conservation; International Fund for Agricultural Development, Grant/Award Number: EB2016/LOT/G.19; Nederlandse Organisatie voor Wetenschappelijk Onderzoek, Grant/Award Number: 863.15.017; Stichting fonds Dr. Christine Buisman; Swedish Research Council Formas, Grant/Award Number: 2017-00430; Wageningen University Fund; Kenya Cereal Enhancement Programme-Climatic Resilient Agricultural Livelihoods (KCEP-CRAL) Programme, Grant/Award Number: MOA/SDA/TA/8/31

Handling Editor: Lars Brudvig

## Abstract

1. Land degradation is a major threat to food security in Sub Saharan Africa. Low infiltration rates in degraded soils increase the risk of surface runoff and decrease soil and groundwater recharge, resulting in further loss of soil fertility, water scarcity and crop failure. Increasing woody vegetation typically enhances soil infiltrability but little is known about how species may have differential effects on the soil hydrological properties. The aim of this study is to understand how woody vegetation and its functional properties affect soil fertility and infiltrability.
2. We measured field-saturated soil hydraulic conductivity ( $K_{fs}$ ) and soil organic carbon (SOC) in 38 plots across agricultural landscapes in Muminji, Kenya. Woody vegetation and land use inventories took place and species functional traits were measured on the 63 most abundant species. We systematically tested the effects of vegetation quantity (aboveground woody biomass and vegetation cover) and quality (functional properties and diversity) on soil health ( $K_{fs}$  as a proxy for soil infiltrability and SOC for soil fertility).
3. We found that both vegetation quantity and quality affected soil health. Aboveground woody biomass increased the  $K_{fs}$  and we found a nearly significant positive effect of vegetation cover on SOC. Woody plants with a low leaf thickness positively affected  $K_{fs}$  and a nearly significant negative effect of wood moisture content on SOC was found.
4. *Synthesis and applications.* This study demonstrates that the systematic assessment of vegetation can lead to evidence-based recommendations to guide land restoration. We found that avoiding bare soil and promoting woody plants, while favouring species with thin leaves and avoiding species with a very low wood density and water storage strategy, is beneficial for soil health across agricultural landscapes in East African drylands.

## KEYWORDS

agricultural landscapes, degradation, East Africa, functional traits, Kenya, restoration, soil infiltration, soil organic carbon

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

## 1 | INTRODUCTION

Land degradation threatens the food security of 2.6 billion people worldwide (Fleitmann et al., 2007; Jie et al., 2002) and it may involve an increased bulk density, a reduced soil infiltrability and low C and N concentrations (cf. Nyberg et al., 2012). Land degradation in general (Sanchez, 2002), and reduced soil infiltrability specifically (Falkenmark & Rockström, 2008), is a major cause of crop failure on farms in the degradation-prone drylands of Sub-Saharan Africa. Low infiltration rates decrease soil and groundwater recharge and increase surface runoff and erosion severity (cf. Recha et al., 2012), which negatively impacts food and water security. This problem is expected to exacerbate with climate change as the frequency of heavy precipitation is projected to increase over East Africa (Seneviratne et al., 2012). To adapt to climate change, there is a great need to restore degraded land through improving soil hydrological functioning. In addition, soil organic carbon (SOC) plays a major role in mitigating climate change (Sommer & Bossio, 2014). This study aims to understand how vegetation affects soil infiltrability and SOC and to evaluate the extent to which tree species can be selected to restore soil hydrological functioning in agricultural landscapes based on their functional properties.

Trees can enhance soil infiltrability in two ways. First, trees increase the SOC content (Bayala et al., 2006; Lohbeck et al., 2018), which improves soil structure and aggregation, and ultimately can increase soil infiltrability (Lado et al., 2004). Second, trees may positively affect soil macrofauna abundance and richness due to improved microclimate and soil organic matter content (Zhao & Liu, 2013), and the presence of tree roots and tree-associated soil macrofauna can enhance macropore preferential flow, resulting in a faster flow of water through the soil (Bargués Tobella et al., 2014; Léonard et al., 2004; Marquart et al., 2020).

The increase in infiltrability after tree planting differs between species (Malmer et al., 2010) but little is known about the mechanisms. Here, we will test whether woody plant functional traits, which are indicators of plant functional strategies, affect soil infiltrability and SOC. This knowledge is fundamental to be able to select species with desired properties for restoring ecosystem functionality (e.g. Laughlin, 2014). Functional strategies can be simplified along the acquisitive-conservative axis, which indicates the resource-use strategy of species, including the use of water, and has consequences for effects on soil health indicators (Díaz et al., 2004; Reich, 2014). Species with a conservative resource-use strategy are found on one end of the spectrum, these have low growth rates, high investment in long-lived tissues (Wigley et al., 2016) and tend to slow down decomposition, thereby promoting SOC (de Deyn et al., 2008). Conservative species are less vulnerable to cavitation, hence can tolerate negative leaf water potentials, making them drought tolerant (Bucci et al., 2004; Markesteijn et al., 2011). Species with an acquisitive strategy, found at the other end of the spectrum, grow fast, have short-lived tissues and tend to increase decomposition rates and soil macrofauna abundances (cf. Frouz et al., 2013; Pérez-Harguindeguy et al., 2000). They also increase carbon sequestration

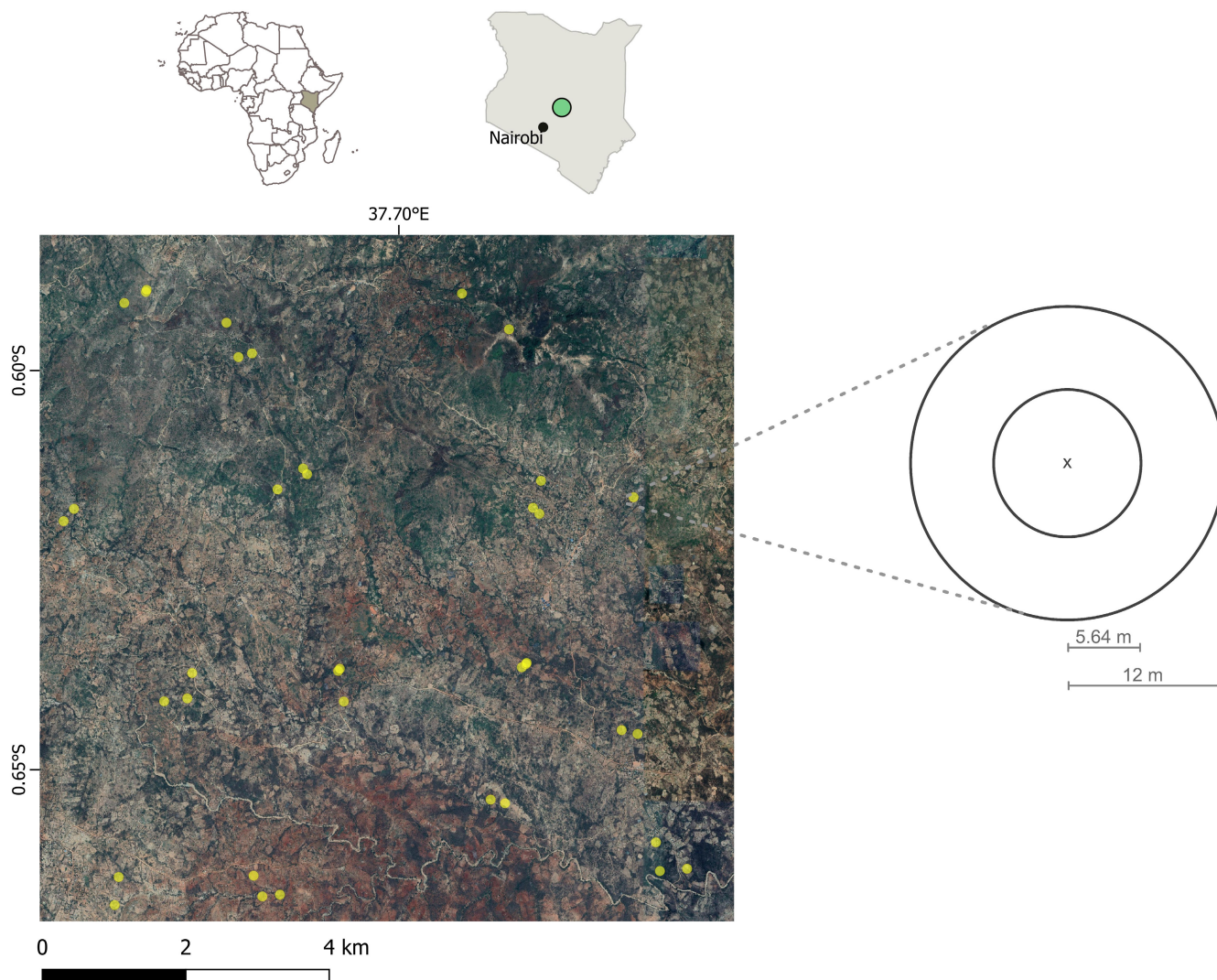
by maintaining high primary productivity, often accompanied by nitrogen fixation, and by enhancing soil macrofauna abundances and microbial activity which could play an important role in SOC stabilization (Bossuyt et al., 2005; Frouz et al., 2013). Acquisitive species may be able to cope with drought by having deeper rooting systems, shedding leaves in the dry season and storing water in the stem (Bucci et al., 2004; Pineda-García et al., 2013; Poorter & Markesteijn, 2008). Besides the functional traits of individual plants, the diversity of the community affects ecosystem functioning (Díaz & Cabido, 2001). Plant functional diversity and plant species richness can positively influence soil infiltrability and SOC by enhancing soil macrofauna diversity (Schuldt et al., 2019), microbial activity (Prommer et al., 2020) and erosion resistance (Wen et al., 2021).

This study was conducted in an agriculture-dominated landscape in the drylands of East Africa, where water is the most critical limiting resource for plant growth, poverty is widespread and climate change poses a threat to people's livelihoods (de Leeuw et al., 2014; Ringler et al., 2010). A systematic landscape-level assessment of soil health (field-saturated soil hydraulic conductivity ( $K_{fs}$ ) and SOC), vegetation properties, land use and soil properties was conducted for 38 plots in Muminji, Kenya. 14 plant functional traits were selected based on their relevance for water-use strategies and effects on SOC and  $K_{fs}$  (Table S1) and measured for the 63 most abundant tree species. As macropore preferential flow decreases with distance from trees (cf. Bargués Tobella et al., 2014; Dunkerley, 2000), vegetation effects were assessed at two spatial scales, to evaluate whether a smaller scale yields stronger effects of woody plants on soil infiltrability. We hypothesized that (1) aboveground woody biomass and vegetation cover increase  $K_{fs}$  and SOC, (2) abundance of plant functional traits related to an acquisitive strategy increase  $K_{fs}$  and SOC, (3) plant functional diversity and species richness increase  $K_{fs}$  and SOC, and (4) effects of the vegetation on  $K_{fs}$  are stronger at the smaller scale.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study took place in a mosaic agricultural landscape in Muminji, Embu district, south-east of Mount Kenya, Kenya (Figure 1). A research licence was granted by the National Commission for Science, Technology and Innovation to conduct research in Kenya: NACOSTI/P/19/57548/30577. Muminji has an average elevation of 1110m, an average annual precipitation of 1120mm, with two rainy seasons from March until May and October until December, and an average temperature of 18.6–21.6°C (en.climate-data.org). No rainfall was recorded during fieldwork, which took place between June and August. The natural vegetation is dominated by the dry-combretum-wooded-grassland vegetation type (van Breugel et al., 2015) in which various broad-leaved *Combretum* species are associated with larger-leaved species of *Terminalia* (Kindt et al., 2015). Smallholder farmers grow crops (e.g. corn, beans, sorghum, cowpea) and economically valuable tree and shrub species (e.g. khat, mango, papaya, citrus, avocado).



**FIGURE 1** Location of the 10×10 km study site and the 38 plots. Each plot has a radius of 12 m and has one subplot in the middle with a radius of 5.64 m.

## 2.2 | Sampling framework

Data collection was based on an adjusted version of the Land Degradation Surveillance Framework (LDSF; Vågen & Winowiecki, 2020). The LDSF framework is built around a hierarchical field survey and sampling protocol. About half of the LDSF plots in Muminji site, which is 10×10 km in size, are cultivated, the other half is fallow land or woodland used for grazing (Winowiecki & Vågen, 2019). The site consisted of fifteen 1 km<sup>2</sup> sampling clusters, and in each cluster one to three plots have been sampled for vegetation properties, soil properties and land use scores. We used a stratified random sampling design: the site was divided into 2.5×2.5 km tiles; the centre point for each cluster within each of the tiles was randomized; and plots were randomly located within the clusters to represent existing variation in topography, land use and vegetation. This resulted in a total of 38 plots 452 m<sup>2</sup> in size (12 m radius). At the centre of each plot, there was a 100 m<sup>2</sup> (5.64 m radius) subplot (Figure 1). We used both the plots and the subplots as the unit of

analysis in this study, and its comparison served to assess the effect of spatial scale.

## 2.3 | Land use practices

For each plot, the impact of agriculture and impact of grazing was visually assessed from 0 (no impact) to 3 (severe impact). Although this method has some subjectivity, the assessment was done by the same people for all plots to ensure consistent scoring (Lohbeck et al., 2020).

## 2.4 | Soil health and inherent soil properties

Soil health, indicated by SOC and  $K_{fs}$ , is influenced by land use, vegetation properties and inherent soil properties (Bruns, 2014). Sand and clay content are indicators of inherent soil properties

that influence vegetation properties but are not influenced by management. These were considered to statistically control for differences in soil inherent properties and to allow making inferences about management. Since  $K_{fs}$  can be affected by SOC (Lado et al., 2004), SOC was as well included in the analysis as a variable explaining  $K_{fs}$ .

Composite soil samples were analysed to estimate SOC (g/kg), sand content (%) and clay content (%). One topsoil (0–20 cm) sample was collected from the centre of the subplot and plot and three topsoil samples were collected from three locations at the edge of the plot and mixed to form a composite topsoil sample for each plot. SOC, sand content and clay content were measured using wet chemistry on 10% of the samples, which were considered reference samples. We made use of calibration models that were developed to predict soil properties of the remaining samples with Mid-Infrared (MIR) spectroscopy using the ICRAF pan-African MIR spectral library (Vågen et al., 2013; Vågen et al., 2016). Midinfrared spectroscopy (MIRS) is becoming a well-established cost-effective method for predicting soil properties (cf. Madari et al., 2006; Reeves III et al., 2006; Vågen & Winowiecki, 2013; Vågen et al., 2016). Topsoil field-saturated hydraulic conductivity ( $K_{fs}$ ) was estimated from infiltration measurements (Nimmo et al., 2009) in the centre of each (sub)plot (Figure 1) using a single-ring infiltrometer (Bouwer, 1986). For detailed methods see Appendix S1.

## 2.5 | Biomass estimations and vegetation cover

All woody plants (height  $\geq 1.50$  m) in all plots and subplots were identified and measured. Additionally, all specimens of *Catha edulis* were included, even if they did not reach 1.50 m, as this species is commonly cultivated and pruned to maintain a height of 1.10 to 1.70 m. The aboveground biomass of trees was calculated using the formula established by Chave et al. (2005), based on the diameter at breast height, height and wood density. The aboveground biomass of shrubs was calculated using the formula established by Conti et al. (2013), based on crown area, height and wood density. Single-stem species were treated as trees and multi-stem species as shrubs.

The canopy density was measured using a spherical densiometer along two linear transects of 24 meter crossing the plot and the subplot, in which measurements were taken every 4 m along each transect. This resulted in thirteen measurements per plot and five per subplot, from which the average canopy closure was calculated for each plot and subplot.

The distance (m) between the nearest woody plant (height  $\geq 1.50$  m) and the infiltration measurement was recorded to test the effect of the distance to the nearest woody plant on  $K_{fs}$ .

The herbaceous cover (herbs and grasses) for each plot and subplot was estimated using a Braun–Blanquet vegetation rating scale that ranges from 0 (bare soil) to 5 (>65% cover; Braun–Blanquet, 1932).

## 2.6 | Functional traits

A total of 2422 trees and shrubs belonging to 146 different species were identified across the 38 plots. 14 functional leaf- and wood traits were selected based on their known importance for the acquisitive-conservative spectrum, for water-use strategies and their effects on soil properties (Table S1). Traits were measured following standardized protocols (Pérez-Harguindeguy et al., 2013), detailed methods on functional traits measurements are presented in Appendix S2. Traits were measured on 63 species that made up at least 80% of the relative woody biomass for each plot and subplot, which is considered representative for the community (Pakeman & Quested, 2007). From the 63 selected species, 60 were identified to species level, *Euphorbia* spp. and *Diospyros* spp. to genus level, and one species (“Murekethaitigo”) was identified with a local name. Five individuals per species were measured for each trait: this is the minimum number recommended for functional traits measurements (Pérez-Harguindeguy et al., 2013). Individuals for traits measurements were selected randomly across the study site and grew under a range of conditions. The trait variation between and within species is visualized in Figure S2.

## 2.7 | Community-level functional properties and diversity

Species-level functional traits of the woody species were scaled to plot- and subplot level by calculating the community weighted mean (CWM) values. The community weighted mean represents the mean of trait values in the community, where each species in the community is weighted by its relative biomass in that plot (Díaz et al., 2007). In addition to CWMs for each of the traits, we also calculated CWMs based on the species scores on the principal components 1 and 2 as indicators of functional strategies. Functional diversity (multidimensional; including all traits) per plot and subplot was calculated using Rao's quadratic entropy (Botta-Dukát, 2005). Functional properties were calculated at the plot and the subplot level using the R package “FD” (Laliberté et al., 2014). Species richness was obtained by counting the number of woody plant species ( $\geq 1.50$  m high) in each plot and subplot.

## 2.8 | Statistical analysis

A principal component analysis was carried out on species (63) and their functional traits (14) to assess functional strategies and trade-offs. 120 out of 882 trait values were missing (Appendix S3), these were estimated using the impute function in Hmisc package (Harrell Jr., 2021). A varimax rotation was applied to the PCA to enhance interpretation of the principal components.

Multiple linear regressions were used (R package STATS, R Core Team, 2020) to systematically test for the effects of inherent soil properties, SOC (only for  $K_{fs}$ ), land use, vegetation quantity, CWMs



of functional traits and diversity on  $K_{fs}$  and on SOC across the plots. Plots or subplots were used as the unit of replication ( $N = 38$ ). Community weighted means of functional traits and functional diversity (RaoQ) were only available for 37 plots.

We used alternative models that represent increased complexity: the simplest model included soil inherent properties (model 1), SOC (only for  $K_{fs}$ ) (model 2), after which land use practices (model 3), herbaceous cover (model 4), woody vegetation quantities (model 5), CWMs of functional traits (model 6) and diversity variables (model 7) were added in a stepwise approach (Díaz et al., 2007). For each of the variable groups, several indicator variables were added one by one, representing alternative models. This resulted in a total of 27 alternative models for  $K_{fs}$  plot level and subplot level and 25 alternative models for SOC (Table S2). The optimal model for each soil health variable was selected based on Akaike information criterion (AICc; Burnham & Anderson, 2002). When AIC between models did not differ significantly ( $\Delta AICc < 2$ ), the model with the highest  $R^2$  was chosen (Nakagawa & Schielzeth, 2013). As we only had vegetation trait data for 34 replicates (model 6 and 7) at the subplot level, the comparison was made using the same subset of observations at the subplot and plot level for  $K_{fs}$ . Statistical analyses were performed in R version 4.0.1 (R Core Team, 2020).

### 3 | RESULTS

#### 3.1 | Principal component analysis

Dimension 1 and 2 of the PCA explained 56.7% of the variation in 14 functional traits across 63 species (Figure 2). Dimension 1 can be defined as the drought tolerance-avoidance spectrum characterized

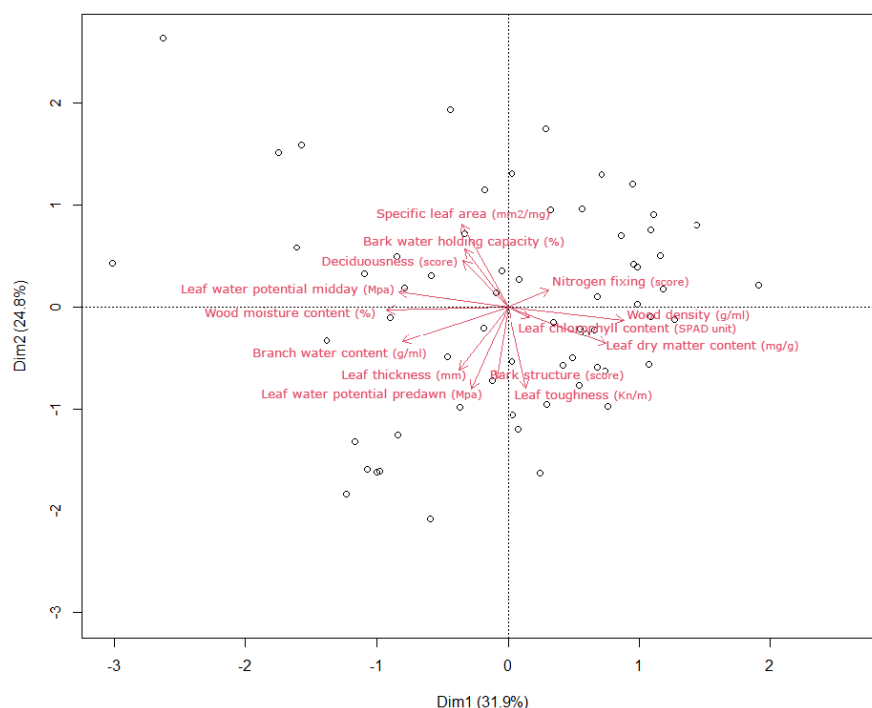
by drought avoidant, (partly) deciduous species with high specific leaf area, high wood moisture content at the left side of the spectrum (negative values) and drought tolerant species with more negative midday leaf water potentials, high wood density, and high leaf dry matter content at the right side of the spectrum (positive values). Dimension 2 can be defined as the acquisitive to conservative resource-use spectrum with acquisitive species with a high specific leaf area, smooth bark, thin and soft leaves at the upper part of the spectrum (positive values), and conservative species with a low specific leaf area, rough bark, thick and tough leaves at the lower part of the spectrum (negative values).

#### 3.2 | Optimal models explaining $K_{fs}$ and SOC

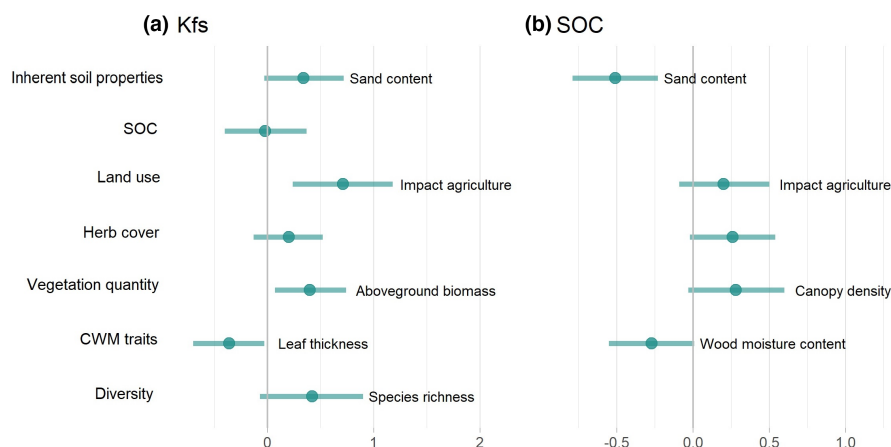
The best model for  $K_{fs}$  was at plot level.  $K_{fs}$  increased with above-ground woody biomass and impact of agriculture and decreased with community-weighted mean of leaf thickness. Sand content and species richness had a nearly significant positive effect and herb cover and SOC did not affect  $K_{fs}$  (Figure 3a and Figure S3).

The most important factor predicting SOC was sand content, where SOC significantly decreased with sand content. The proxies for vegetation quantity in the optimal model, which are herb cover and canopy density, were not significant but showed a nearly significant positive trend. The community weighted mean of wood moisture content had a nearly significant negative effect on SOC. Land use did not affect SOC (Figure 3b and Figure S4).

See Table S3 for the fixed-effects statistics for the optimal models explaining  $K_{fs}$  and SOC and Table S4 for summary statistics of the five best alternative models for  $K_{fs}$  at plot level,  $K_{fs}$  at subplot level and SOC.



**FIGURE 2** Principal Component Analysis separating all species ( $N = 63$ ) based on their functional traits ( $N = 14$ ).



**FIGURE 3** Effect sizes of variables in the optimal models explaining  $K_{fs}$  and SOC. Given are the standardized beta for each variable (point) and the 95% confidence intervals. Vegetation quantity, CWM traits and diversity are woody vegetation variables.

## 4 | DISCUSSION

### 4.1 | Tree resource-use and water-use strategies

The principal component analysis showed that the water-use spectrum was partially related to the acquisitive-conservative resource-use spectrum, which coincides with previous findings (Poorter & Markesteijn, 2008; Reich, 2014). The PCA shows that conservative traits like high wood density, high leaf dry matter content, tough leaves and being evergreen are related to the ability to withstand low midday leaf water potentials (Figure 2) and thus to drought tolerance (Markesteijn et al., 2011). The PCA also shows that acquisitive traits like high specific leaf area, low wood density and soft leaves are related to deciduousness and thus to drought avoidance (Figure 2). Water storage is another drought coping mechanism that was identified and is related to a high wood moisture content, low wood density and the ability to maintain stable leaf water potentials (Figure 2). These species can take up large amounts of water under wet circumstances (Pineda-García et al., 2016) and have water storage as a drought survival mechanism (Pineda-García et al., 2013). A fourth mechanism, water exploitation, is characterized by thick leaves and high predawn leaf water potentials (Figure 2). Their drought survival strategy depends on deep rooting systems, as indicated by the less negative predawn leaf water potentials (Pérez-Harguindeguy et al., 2013).

### 4.2 | Effect of vegetation quantity

We showed that after controlling for soil inherent properties (sand content), both soil infiltrability and SOC are affected by vegetation quantity, which supports that increasing tree cover is suitable for restoring soil health.  $K_{fs}$  increased with aboveground woody biomass (Figure 3a), which corresponds with earlier findings where the presence of trees positively affected soil infiltrability (Bargués Tobella et al., 2014; Bonnesoeur et al., 2019; Ilstedt et al., 2007). Aboveground biomass is strongly related to the belowground root biomass (Cheng & Niklas, 2007). We hypothesized that the positive effect of vegetation on soil infiltrability could be caused either by

increased aggregate stability due to enhanced SOC content (Lado et al., 2004; Lohbeck et al., 2018), or by increased preferential flow along channels created by roots and tree-associated soil macrofauna (Bargués Tobella et al., 2014; Dunkerley, 2000; Marquart et al., 2020). As SOC did not have an effect in the optimal infiltration-model, probably macropores from root channels and tree-associated soil macrofauna play a key role in explaining our result (Marquart et al., 2020).

The optimal SOC model showed weak positive effects of herb cover and canopy density, after controlling for sand content (Figure 3b). Vegetation cover reduces the rainfall impact on the soil, thereby reducing soil erosion and runoff which may prevent losses of organic carbon (cf. Breshears et al., 2009; Lohbeck et al., 2018). A positive effect of aboveground woody biomass on SOC was expected (cf. Bayala et al., 2006; Lohbeck et al., 2018) but did not play a role in the optimal SOC-model.

### 4.3 | Effect of vegetation quality

Soil infiltrability was best explained by the most complex model at plot-level which included both vegetation quantity and vegetation quality variables.  $K_{fs}$  increases with the abundance of thin-leaved woody plants, indicating an acquisitive functional strategy, which was in line with our expectation (Figure 3a). We argued the positive influence of acquisitive traits on soil infiltrability would be caused by an increase in soil macrofauna abundance due to the presence of a high litter quality. Acquisitive leaf traits (high SLA, low toughness and thickness) are strongly related to a low leaf C:N ratio, which increases litter decomposition rates (Bakker et al., 2011; Pérez-Harguindeguy et al., 2000) and earthworm abundance (Frouz et al., 2013). As earthworm abundance enhances soil macroporosity it is expected earthworms positively affect soil infiltrability (van Schaik et al., 2014). However, further experimental research is needed to confirm the causality of the relation between thin leaves, earthworm abundance, macroporosity and soil infiltrability. Earthworm casts are known to increase SOC and aggregate stability, further improving soil structure and soil infiltrability (Bossuyt et al., 2005; Frouz et al., 2013). However,

SOC did not have an effect in the optimal model for steady-state soil infiltrability. Possibly, the effect of earthworms is restricted to burrows and does not influence the surrounding soil (cf. Don et al., 2008). Alternatively, the increased stabilization of SOC by soil macrofauna at low C:N litter ratio could be counteracted by the increased decomposition rate at a low C:N litter ratio reducing the SOC content (Mueller et al., 2015).

We hypothesized that plant diversity would increase macrofauna abundances, through niche differentiation, and thereby positively affect soil infiltrability (Schuldt et al., 2019). Although the optimal model explaining  $K_{fs}$  indeed showed a weak positive effect of species richness (Figure 3a), the effect of community-weighted trait means were more important than diversity-effects. This is in line with the review of Korboulewsky et al. (2016) who show that soil organism abundance and diversity is strongly affected by the presence of certain tree species rather than their diversity and coincides with the 'mass ratio hypothesis' (Grime, 1998), stating that trait values of the dominant species have a disproportional effect on ecosystem processes.

The optimal model for SOC showed a weak negative effect of wood moisture content (Figure 3b). A high wood moisture content is related to species that store water in their stem and have a low wood density (Figure 2). It could be argued the negative trend of wood moisture content on SOC is related to an increased carbon mineralization due to a high litter quality and moisture content, similar to what Mori et al. (2014) found for low wood densities and high water permeability, which may reduce SOC (Lin et al., 2016). Alternatively, wood moisture content might be related to specific root traits reducing SOC stabilization (Poirier et al., 2018). Root traits, such as root C:N ratio and fine root distribution are expected to play a key role in explaining how trees influence soil properties (Hao et al., 2020; Poirier et al., 2018) and were not measured in this study, further research is needed to clarify the relation between root traits, SOC and soil infiltrability.

Our study demonstrates that functional properties of the vegetation have an effect on soil health. Species with thin leaves, which is related to both drought avoidance (semi-deciduous) and drought tolerance strategies (Figure 2), enhanced soil infiltrability. Species with a high wood moisture content, which is related to the water storage strategy and a low wood density (Figure 2), reduced SOC. Our results suggest that promoting woody plants with thin leaves, thereby avoiding species with a very low wood density and water storage strategy, may benefit overall soil health.

#### 4.4 | Effect of land use

The optimal model explaining  $K_{fs}$  included the land use variable impact of agriculture.  $K_{fs}$  increases with the impact of agricultural practices (Figure 3a), which may point to the practice of tillage. Soil tillage can increase porosity and decrease bulk density, thereby increasing infiltration rates (Amami et al., 2021). However, soil tillage may also decrease SOC and aggregate stability which negatively affects soil

infiltrability (Sithole et al., 2019). In this study however, we found no significant effect of land use on SOC (Figure 3b).

#### 4.5 | Effect of scale

Unexpectedly,  $K_{fs}$  was better explained at plot level (452 m<sup>2</sup>) than at subplot level (100 m<sup>2</sup>). Previous studies found that vegetation effects on soil infiltrability decreases with distance from woody plants (Bargués Tobella et al., 2014; Dunkerley, 2000). A possible explanation is that our subplots may have been too small (100 m<sup>2</sup>) and that the effect on steady-state soil infiltrability is better expressed at the somewhat larger (452 m<sup>2</sup>) plot-scale. This matters for restoration planning as the relatively large scale at which trees improve soil infiltration gives opportunities for agroforestry design in which light and water competition with crops is limited by optimal spacing of trees. Future research should further study optimal tree spacing by including more varied scales of analysis or a continuous gradient of distance to trees.

#### 4.6 | Implications for restoration of soil health across agricultural landscapes

Entering the UN decade on ecosystem restoration, there is a great need for evidence-based restoration solutions. The drylands of Sub-Saharan Africa are much affected by land degradation, causing crop failure and food insecurity. This study emphasizes the importance of woody and non-woody vegetation quantity and quality for soil health. Since farmers directly depend on healthy soils to sustain their livelihoods, our results may guide management and tree species selection in agricultural landscapes. To increase soil infiltrability and SOC, we recommend farmers in Kenyan drylands to avoid bare soil and promote trees on their farms (i.e. agroforestry), specifically those with thin leaves, while avoiding trees that store water in the stems.

#### AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the methodology. Lotte Patty Mens, Aida Bargués-Tobella, Leigh Ann Winowiecki and Tor-Gunnar Vågen collected the data. Lotte Patty Mens and Madelon Lohbeck analysed the data and led the writing of this manuscript. All authors contributed to the drafts and gave final approval for publication.

#### ACKNOWLEDGEMENTS

We are grateful to the farmers and local officials for granting us access to their properties. We greatly acknowledge Jared Otieno Onyango, John Thiong'o Maina, Michael Munyi, Elias Njuki, Henry Murimi Kinyua and Ian Murithi for assistance during field campaigns and the staff of the ICRAF Soil and Plant Spectroscopy Lab for processing soil samples. This study was conducted as part of the Kenya Cereal Enhancement Programme-Climate

Resilient Agricultural Livelihoods (KCEP-CRAL) Programme supported by the Government of Kenya and the International Fund for Agricultural Development (IFAD) within the Adaptation for Smallholder Agriculture Programme (ASAP), and the CGIAR Program on Forests, Trees and Agroforestry (FTA). LPM acknowledges financial support from Stichting Fonds Dr. Christine Buisman, FONA Nature Conservation and University Fund Wageningen. ABT acknowledges funding from the Swedish Research Council Formas, grant number 2017-00430. ML acknowledges support from research programme ALW-VENI (863.15.017), financed by the Netherlands Organization for Scientific Research (NWO).

## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Vegetation quantity and trait data are available from the 4TU database: <https://doi.org/10.4121/19635243>. LDSF soil and land use data are available from World Agroforestry (ICRAF) Database: <https://doi.org/10.34725/DVN/CBHCKS> (Winowiecki et al., 2021).

## ORCID

Lotte Patty Mens  <https://orcid.org/0000-0002-6977-5635>

Aida Bargués-Tobella  <https://orcid.org/0000-0001-5632-4061>

Frank Sterck  <https://orcid.org/0000-0001-7559-6572>

Tor-Gunnar Vågen  <https://orcid.org/0000-0002-8699-731X>

Leigh Ann Winowiecki  <https://orcid.org/0000-0001-5572-1284>

Madelon Lohbeck  <https://orcid.org/0000-0002-3959-1800>

## REFERENCES

- Amami, R., Ibrahim, K., Sher, F., Milham, P., Ghazouani, H., Chehaibi, S., Hussain, Z., & Iqbal, H. M. N. (2021). Impacts of different tillage practices on soil water infiltration for sustainable agriculture. *Sustainability*, 13(6), 3155. <https://doi.org/10.3390/su13063155>
- Bakker, M. A., Carreño-Rocabado, G., & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Functional Ecology*, 25(3), 473–483. <https://doi.org/10.1111/j.1365-2435.2010.01802.x>
- Bargués Tobella, A., Reese, H., Almaw, A., Bayala, J., Malmer, A., Laudon, H., & Ilstedt, U. (2014). The effect of trees on preferential flow and soil infiltrability in an agroforestry parkland in semiarid Burkina Faso. *Water Resources Research*, 50(4), 3342–3354. <https://doi.org/10.1002/2013WR015197>
- Bayala, J., Balesdent, J., Marol, C., Zapata, F., Teklehaimanot, Z., & Quedraogo, S. J. (2006). Relative contribution of trees and crops to soil carbon content in a parkland system in Burkina Faso using variations in natural  $^{13}\text{C}$  abundance. *Nutrient Cycling in Agroecosystems*, 76, 193–201. <https://doi.org/10.1007/s10705-005-1547-1>
- Bonnesoeur, V., Locatelli, B., Guariguata, M. R., Ochoa-Tocachi, B. F., Vanacker, V., Mao, Z., Stokes, A., & Mathez-Stiefel, S.-L. (2019). Impacts of forests and forestation on hydrological services in the Andes: A systematic review. *Forest Ecology and Management*, 433, 569–584. <https://doi.org/10.1016/j.foreco.2018.11.033>
- Bossuyt, H., Six, J., & Hendrix, P. F. (2005). Protection of soil carbon by microaggregates within earthworm casts. *Soil Biology and Biochemistry*, 37(2), 251–258. <https://doi.org/10.1016/j.soilbio.2004.07.035>
- Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16(5), 533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>
- Bouwer, H. (1986). Intake rate: Cylinder infiltrometer. *Methods of Soil Analysis: Part 1 Physical and Mineralogical Methods*, 5, 825–844. <https://doi.org/10.2136/sssabookser5.1.2ed.c32>
- Braun-Blanquet, J. (1932). Plant sociology. In D. M. Raup & D. Jablonski (Eds.), *The study of plant communities*. McGraw-Hill.
- Breshears, D. D., Whicker, J. J., Zou, C. B., Field, J. P., & Allen, C. D. (2009). A conceptual framework for dryland aeolian sediment transport along the grassland-forest continuum: Effects of woody plant canopy cover and disturbance. *Geomorphology*, 105(1–2), 28–38. <https://doi.org/10.1016/j.geomorph.2007.12.018>
- Bruns, M. A. (2014). Sustainable soil health. In *Plant biotechnology: Experience and future prospects* (Vol. 9783319068923, pp. 209–223). Springer International Publishing. [https://doi.org/10.1007/978-3-319-06892-3\\_17](https://doi.org/10.1007/978-3-319-06892-3_17)
- Bucci, S. J., Goldstein, G., Meinzer, F. C., Scholz, F. G., Franco, A. C., & Bustamante, M. (2004). Functional convergence in hydraulic architecture and water relations of tropical savanna trees: From leaf to whole plant. *Tree Physiology*, 24(8), 891–899. <https://doi.org/10.1093/treephys/24.8.891>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.
- Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B. W., Ogawa, H., Puig, H., Riéra, B., & Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145(1), 87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- Cheng, D. L., & Niklas, K. J. (2007). Above-and below-ground biomass relationships across 1534 forested communities. *Annals of Botany*, 99(1), 95–102. <https://doi.org/10.1093/aob/mcl206>
- Conti, G., Enrico, L., Casanoves, F., & Díaz, S. (2013). Shrub biomass estimation in the semiarid Chaco for- Est: A contribution to the quantification of an underrated carbon stock. *Annals of Forest Science*, 70(5), 515–524. <https://doi.org/10.1007/s13595-013-0285-9>
- de Deyn, G. B., Cornelissen, J. H., & Bardgett, R. D. (2008). Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, 11(5), 516–531. <https://doi.org/10.1111/j.1461-0248.2008.01164.x>
- de Leeuw, J., Njenga, M., Wagner, B., & Iiyama, M. (2014). *Treesilience: An as*. The WORLD AGROFORESTRY CENTRE (ICRAF).
- Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11), 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-Martí, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M. C., Shirvany, F. A., ... Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, 15(3), 295–304. <https://doi.org/10.1111/j.1654-1103.2004.tb02266.x>
- Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., & Robson, T. M. (2007). Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences of the United States of America*, 104(52), 20684–20689. <https://doi.org/10.1073/pnas.0704716104>
- Don, A., Steinberg, B., Schöning, I., Pritsch, K., Joschko, M., Gleixner, G., & Schulze, E. D. (2008). Organic carbon sequestration in earthworm burrows. *Soil Biology and Biochemistry*, 40(7), 1803–1812. <https://doi.org/10.1016/j.soilbio.2008.03.003>



- Dunkerley, D. (2000). Hydrologic effects of dryland shrubs: Defining the spatial extent of modified soil water uptake rates at an Australian desert site. *Journal of Arid Environments*, 45(2), 159–172. <https://doi.org/10.1006/jare.2000.0636>
- Falkenmark, M., & Rockström, J. (2008). Building resilience to drought in desertification-prone savannas in sub-Saharan Africa: The water perspective. In *Natural resources forum* (Vol. 32, No. 2, pp. 93–102). Blackwell Publishing Ltd. <https://doi.org/10.1111/j.1477-8947.2008.00177.x>
- Fleitmann, D., Dunbar, R. B., McCulloch, M., Mudelsee, M., Vuille, M., McClanahan, T. R., Cole, J. E., & Eggins, S. (2007). East African soil erosion recorded in a 300-year-old coral colony from Kenya. *Geophysical Research Letters*, 34(4), 1–5. <https://doi.org/10.1029/2006GL028525>
- Frouz, J., Livečková, M., Albrechtová, J., Chroňáková, A., Cajthaml, T., Pižl, V., Hánel, L., Starý, J., Baldrian, P., Lhotáková, Z., Šimáčková, H., & Cepáková, Š. (2013). Is the effect of trees on soil properties mediated by soil fauna? A case study from post-mining sites. *Forest Ecology and Management*, 309, 87–95. <https://doi.org/10.1016/j.foreco.2013.02.013>
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, 86(6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Hao, H. X., Wei, Y. J., Cao, D. N., Guo, Z. L., & Shi, Z. H. (2020). Vegetation restoration and fine roots promote soil infiltrability in heavy-textured soils. *Soil and Tillage Research*, 198, 104542. <https://doi.org/10.1016/j.still.2019.104542>
- Harrell Jr., F. E. (2021). Hmisc: Harrell Miscellaneous. with contributions from Charles Dupont and many others. R package version 4.5–0. <https://CRAN.R-project.org/package=Hmisc>
- Ilstedt, U., Malmer, A., Verbeeten, E., & Murdiyoso, D. (2007). The effect of afforestation on water infiltration in the tropics: A systematic review and meta-analysis. *Forest Ecology and Management*, 251(1–2), 45–51. <https://doi.org/10.1016/j.foreco.2007.06.014>
- Jie, C., Jing-Zhang, C., Man-Zhi, T., & Zi-tong, G. (2002). Soil degradation: A global problem endangering sustainable development. *Journal of Geographical Sciences*, 12(2), 243–252. <https://doi.org/10.1007/BF02837480>
- Kindt, R., van Breugel, P., Orwa, C., Lillesø, J. P. B., Jamnadass, R., & Gaudal, L. (2015). *Useful tree species for eastern Africa: A species selection tool based on the VECEA map. Version 2.0*. World Agroforestry (ICRAF) and Forest & Landscape Denmark. <http://vegetationmap4africa.org>
- Korboulewsky, N., Perez, G., & Chauvat, M. (2016). How tree diversity affects soil fauna diversity: A review. *Soil Biology and Biochemistry*, 94, 94–106. <https://doi.org/10.1016/j.soilbio.2015.11.024>
- Lado, M., Paz, A., & Ben-Hur, M. (2004). Organic matter and aggregate size interactions in infiltration, seal formation, and soil loss. *Soil Science Society of America Journal*, 68(3), 935–942. <https://doi.org/10.2136/sssaj2004.9350>
- Labiberté, E., Legendre, P., & B. Shipley. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.
- Laughlin, D. C. (2014). Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*, 17(7), 771–784. <https://doi.org/10.1111/ele.12288>
- Léonard, J., Perrier, E., & Rajot, J. L. (2004). Biological macropores effect on runoff and infiltration: A combined experimental and modelling approach. *Agriculture, Ecosystems & Environment*, 104(2), 277–285. <https://doi.org/10.1016/j.agee.2003.11.015>
- Lin, D., Anderson-Teixeira, K. J., Lai, J., Mi, X., Ren, H., & Ma, K. (2016). Traits of dominant tree species predict local scale variation in forest aboveground and topsoil carbon stocks. *Plant and Soil*, 409(1), 435–446. <https://doi.org/10.1007/s11104-016-2976-0>
- Lohbeck, M., Albers, P., Boels, L. E., Bongers, F., Morel, S., Sinclair, F., Takoutsing, B., Vågen, T. G., Winowiecki, L. A., & Smith-Dumont, E. (2020). Drivers of farmer-managed natural regeneration in the Sahel. Lessons for restoration. *Scientific Reports*, 10(1), 1–11. <https://doi.org/10.1038/s41598-020-70746-z>
- Lohbeck, M., Winowiecki, L., Aynekulu, E., Okia, C., & Vågen, T. G. (2018). Trait-based approaches for guiding the restoration of degraded agricultural landscapes in East Africa. *Journal of Applied Ecology*, 55(1), 59–68. <https://doi.org/10.1111/1365-2664.13017>
- Madari, B. E., Reeves, J. B., Machado, P. L. O. A., Guimarães, C. M., Torres, E., & McCarty, G. W. (2006). Mid- and near-infrared spectroscopic assessment of soil compositional parameters and structural indices in two Ferralsols. *Geoderma*, 136, 245–259. <https://doi.org/10.1016/j.geoderma.2006.03.026>
- Malmer, A., Murdiyoso, D., Bruijnzeel, L. A., & Ilstedt, U. (2010). Carbon sequestration in tropical forests and water: A critical look at the basis for commonly used generalizations. *Global Change Biology*, 16(2), 599–604. <https://doi.org/10.1111/j.1365-2486.2009.01984.x>
- Markestijn, L., Poorter, L., Paz, H., Sack, L., & Bongers, F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment*, 34(1), 137–148. <https://doi.org/10.1111/j.1365-3040.2010.02231.x>
- Marquart, A., Eldridge, D. J., Geissler, K., Lobas, C., & Blaum, N. (2020). Interconnected effects of shrubs, invertebrate-derived macropores and soil texture on water infiltration in a semi-arid savanna range land. *Land Degradation & Development*, 31(16), 2307–2318. <https://doi.org/10.1002/ldr.3598>
- Mori, S., Itoh, A., Nanami, S., Tan, S., Chong, L., & Yamakura, T. (2014). Effect of wood density and water permeability on wood decomposition rates of 32 Bornean rainforest trees. *Journal of Plant Ecology*, 7(4), 356–363. <https://doi.org/10.1093/jpe/rtt041>
- Mueller, K. E., Hobbie, S. E., Chorover, J., Reich, P. B., Eisenhauer, N., Castellano, M. J., Chadwick, O. A., Dobies, T., Hale, C. M., Jagodziński, A. M., Kałucka, I., Kieliszewska-Rokicka, Modrzyński, J., Rozen, A., Skorupski, M., Sobczyk, Ł., Stasińska, M., Trocha, L. K., Weiner, J., ... Oleksyn, J. (2015). Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species. *Biogeochemistry*, 123(3), 313–327. <https://doi.org/10.1007/s10533-015-0083-6>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Nimmo, J. R., Schmidt, K. M., Perkins, K. S., & Stock, J. D. (2009). Rapid measurement of field-saturated hydraulic conductivity for areal characterization. *Vadose Zone Journal*, 8(1), 142–149. <https://doi.org/10.2136/vzj2007.0159>
- Nyberg, G., Tobella, A. B., Kinyangi, J., Ilstedt, U., & van Meerveld, I. (2012). Soil property changes over a 120-yr chronosequence from forest to agriculture in western Kenya. *Hydrology & Earth System Sciences*, 16(7), 2085–2094. <https://doi.org/10.5194/hess-16-2085-2012>
- Pakeman, R. J., & Quedstedt, H. M. (2007). Sampling plant functional traits: What proportion of the species need to be measured? *Applied Vegetation Science*, 10(1), 91–96. <https://doi.org/10.1111/j.1654-109X.2007.tb00507.x>
- Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J. H., Vendramini, F., Cabido, M., & Castellanos, A. (2000). Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in Central Argentina. *Plant and Soil*, 218(1–2), 21–30.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., & Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. <https://doi.org/10.1071/BT12225>

- Pineda-García, F., Paz, H., & Meinzer, F. C. (2013). Drought resistance in early and late secondary successional species from a tropical dry forest: The interplay between xylem resistance to embolism, sapwood water storage and leaf shedding. *Plant, Cell & Environment*, 36(2), 405–418. <https://doi.org/10.1111/j.1365-3040.2012.02582.x>
- Pineda-García, F., Paz, H., Meinzer, F. C., & Angeles, G. (2016). Exploiting water versus tolerating drought: Water-use strategies of trees in a secondary successional tropical dry forest. *Tree Physiology*, 36(2), 208–217. <https://doi.org/10.1093/treephys/tpv124>
- Poirier, V., Roumet, C., & Munson, A. D. (2018). The root of the matter: Linking root traits and soil organic matter stabilization processes. *Soil Biology and Biochemistry*, 120, 246–259. <https://doi.org/10.1016/j.soilbio.2018.02.016>
- Poorter, L., & Markesteijn, L. (2008). Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, 40(3), 321–331. <https://doi.org/10.1111/j.1744-7429.2007.00380.x>
- Prommer, J., Walker, T. W., Wanek, W., Braun, J., Zezula, D., Hu, Y., Hofhansl, F., & Richter, A. (2020). Increased microbial growth, biomass, and turnover drive soil organic carbon accumulation at higher plant diversity. *Global Change Biology*, 26(2), 669–681. <https://doi.org/10.1111/gcb.14777>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Recha, J. W., Lehmann, J., Walter, M. T., Pell, A., Verchot, L., & Johnson, M. (2012). Stream discharge in tropical headwater catchments as a result of forest clearing and soil degradation. *Earth Interactions*, 16(13), 1–18. <https://doi.org/10.1175/2012EI000439.1>
- Reeves, J. B., III, Follett, R. F., McCarty, G. W., & Kimble, J. M. (2006). Can near or mid-infrared diffuse reflectance spectroscopy be used to determine soil carbon pools? *Communications in Soil Science and Plant Analysis*, 37, 2307–2325. <https://doi.org/10.1080/00103620600819461>
- Reich, P. B. (2014). The world-wide ‘fast-slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Ringler, C., Zhu, T., Cai, X., Koo, J., & Wang, D. (2010). Climate change impacts on food security in sub-Saharan Africa. IFPRI Discussion Paper No. 01042, International Food Policy Research Institute (IFPRI), Washington DC, USA, 17 pp.
- Sanchez, P. A. (2002). Soil fertility and hunger in Africa. *Science*, 295(5562), 2019–2020. <https://doi.org/10.1126/science.1065256>
- Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Bachman, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L. R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., ... Eisenhauer, N. (2019). Multiple plant diversity components drive consumer communities across ecosystems. *Nature Communications*, 10(1), 1–11. <https://doi.org/10.1038/s41467-019-09448-8>
- Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., Luo, Y., Marengo, J., McInnes, K., Rahimi, M., Reichstein, M., Sorteberg, A., Vera, C., & Zhang, X. (2012). Changes in climate extremes and their impacts on the natural physical environment. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, Mastrandrea, M. D., Mach, K. J., Plattner, G.-K., Allen, S. K., Tignor, M., & Midgley, P. M. (Eds.), *Managing the risks of extreme events and disasters to advance climate change adaptation*. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC). (pp. 109–230). Cambridge University Press.
- Sithole, N. J., Magwaza, L. S., & Thibaud, G. R. (2019). Long-term impact of no-till conservation agriculture and N-fertilizer on soil aggregate stability, infiltration and distribution of C in different size fractions. *Soil and Tillage Research*, 190, 147–156. <https://doi.org/10.1016/j.still.2019.03.004>
- Sommer, R., & Bossio, D. (2014). Dynamics and climate change mitigation potential of soil organic carbon sequestration. *Journal of Environmental Management*, 144, 83–87. <https://doi.org/10.1016/j.jenvman.2014.05.017>
- Vågen, T. G., & Winowiecki, L. A. (2020). *The land degradation surveillance framework (LDSF) Field guide*. World Agroforestry (ICRAF).
- Vågen, T.-G., & Winowiecki, L. A. (2013). Mapping of soil organic carbon stocks for spatially explicit assessments of climate change mitigation potential. *Environmental Research Letters*, 8, 015011. <https://doi.org/10.1088/1748-9326/8/1/015011>
- Vågen, T.-G., Winowiecki, L. A., Abegaz, A., & Hadgu, K. M. (2013). Landsat-based approaches for mapping of land degradation prevalence and soil functional properties in Ethiopia. *Remote Sensing of Environment*, 134, 266–275.
- Vågen, T. G., Winowiecki, L. A., Tondoh, J. E., Desta, L. T., & Gumbricht, T. (2016). Mapping of soil properties and land degradation risk in Africa using MODIS reflectance. *Geoderma*, 263, 216–225. <https://doi.org/10.1016/j.geoderma.2015.06.023>
- van Breugel, P., Kindt, R., Lillesø, J. P. B., Bingham, M., Demissew, S., Dudley, C., Friis, I., Gachathi, F., Kalema, J., Mbago, F., Moshi, H. N., Mulumba, J., Namaganda, M., Ndangalasi, H. J., Ruffo, C. K., Védaste, M., Jamnadass, R., & Gaudal, L. (2015). *Potential natural vegetation map of eastern Africa (Burundi, Ethiopia, Kenya, Malawi, Rwanda, Tanzania, Uganda and Zambia)*. Version 2.0. Forest and Landscape (Denmark) and World Agroforestry (ICRAF). <http://vegetationmap4africa.org>
- van Schaik, L., Palm, J., Klaus, J., Zehe, E., & Schröder, B. (2014). Linking spatial earthworm distribution to macropore numbers and hydrological effectiveness. *Ecohydrology*, 7(2), 401–408. <https://doi.org/10.1002/eco.1358>
- Wen, Z., Zheng, H., Zhao, H., Liu, L., & Ouyang, Z. (2021). Species compositional, structural and functional diversity exerts different effects on soil erosion caused by increased rainfall intensity in Chinese tropical forests. *Plant and Soil*, 465(1), 97–108. <https://doi.org/10.1007/s11104-021-04980-3>
- Wigley, B. J., Slingsby, J. A., Díaz, S., Bond, W. J., Fritz, H., & Coetsee, C. (2016). Leaf traits of African woody savanna species across climate and soil fertility gradients: Evidence for conservative versus acquisitive resource-use strategies. *Journal of Ecology*, 104(5), 1357–1369. <https://doi.org/10.1111/1365-2745.12598>
- Winowiecki, L. A., & Vågen, T. G. (2019). *Undertaking a biophysical baseline survey and annual tracking of ecosystem health for the Kenya cereal enhancement programme-climate resilient agricultural livelihoods window*. World Agroforestry (ICRAF).
- Winowiecki, L. A., Vågen, T. G., Tobella-Bargues, A., Magaju, C., Muriuki, J., & Mwaniki, A. (2021). *Biophysical baseline assessment within the KCEP-CRAL action areas in Kenya, using the LDSF*. World Agroforestry (ICRAF), V2, UNF:6:U5BJBc7Ju8coHHuO6ptCEA== [fileUNF]. <https://doi.org/10.34725/DVN/CBHCK5>
- Zhao, H. L., & Liu, R. T. (2013). The “bug Island” effect of shrubs and its formation mechanism in Horqin sand land, Inner Mongolia. *Catena*, 105, 69–74. <https://doi.org/10.1016/j.catena.2013.01.009>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Mens, L. P., Bargués-Tobella, A., Sterck, F., Vågen, T.-G., Winowiecki, L. A., & Lohbeck, M. (2023). Towards effectively restoring agricultural landscapes in East African drylands: Linking plant functional traits with soil hydrology. *Journal of Applied Ecology*, 60, 91–100. <https://doi.org/10.1111/1365-2664.14311>