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Trait-based approaches for guiding the restoration of degraded agricultural landscapes in East Africa

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Abstract

1. Functional ecology provides a framework that can link vegetation characteristics of various land uses with ecosystem function. However, this application has been mostly limited to [semi-]natural systems and small spatial scales. Here, we apply functional ecology to five agricultural landscapes in Kenya, Uganda and Ethiopia, and ask to what extent vegetation characteristics contribute to soil functions that are key to farmers' livelihoods.
2. We used the Land Degradation Surveillance Framework (LDSF), a multi-scale assessment of land health. Each LDSF site is a 10 × 10 km landscape in which vegetation cover and erosion prevalence were measured, a tree inventory was carried out, and topsoil (0–20 cm) samples were collected for organic carbon (SOC) analysis in approximately 160 × 1,000 m² plots. Land degradation is a recurring phenomenon across the five landscapes, indicated by high erosion prevalence (67%–99% of the plots were severely eroded). We used mixed models to assess if vegetation cover, above-ground woody biomass and the functional properties of woody vegetation (weighted-mean trait values, functional diversity [FD]) explain variation in SOC and erosion prevalence.
3. We found that the vegetation cover and above-ground biomass had strong positive effects on soil health by increasing SOC and reducing soil erosion. After controlling for cover and biomass, we found additional marginal effects of functional properties where FD was positively associated with SOC and the abundance of invasive species was associated with higher soil erosion.
4. *Synthesis and applications.* This work illustrates how functional ecology can provide much-needed evidence for designing strategies to restore degraded agricultural land and the ecosystem services on which farmers depend. We show that to ensure soil health, it is vital to avoid exposed soil, maintain or promote tree cover, while ensuring functional diversity of tree species, and to eradicate invasive species.

KEYWORDS

agricultural land, agroecology, agroforestry, erosion, functional diversity, functional traits, land degradation, soil health, soil organic carbon, vegetation

1 | INTRODUCTION

The negative impacts of land degradation on productivity, biodiversity and local livelihoods have become undeniable (Pereira et al., 2010; Pimentel & Burgess, 2013). As a consequence, restoration, here defined as the practice of assisting the recovery of degraded ecosystems, is now a global priority (Minnemeyer, Laestadius, Sizer, Saint Laurent, & Potapov, 2011). Restoration provides opportunities to counteract degradation and revive ecosystem functions, including components of biodiversity (Benayas, Newton, Diaz, & Bullock, 2009; Chazdon, 2008) and soil fertility, which is key to farmers' livelihoods (Diemont et al., 2006).

In this study, we assess degradation in agricultural landscapes using two main indicators: soil organic carbon (SOC) and erosion prevalence. SOC is a widely used indicator of soil health as it influences several important soil properties such as cation exchange capacity and water holding capacity (Lal, Griffin, Apt, Lave, & Morgan, 2004). Soil erosion is an indicator of land degradation and is included as a key process leading to loss of SOC and declining soil health and productivity (Dregne, 2002). Both indicators are heavily influenced by management, and unsustainable land use has been shown to reduce SOC and increase erosion, making these suitable indicators for assessing land degradation and soil health (Dregne, 2002; Lal et al., 2004; Vågen, Winowiecki, Abegaz, & Hadgu, 2013; Winowiecki et al., 2015).

Increasing tree cover is a core activity for restoring degraded lands (Lamb, Erskine, & Parrotta, 2005). Recent evidence shows that increasing tree cover in the dry tropics can improve soil function, including water availability (Ilstedt et al., 2016). Furthermore, increasing woody biomass positively affects productivity and litter decomposition rates in regenerating forests (Lohbeck, Poorter, Martínez-Ramos, & Bongers, 2015) and SOC in agroforestry systems (Hombegowda, van Straaten, Köhler, & Hölscher, 2016; Lorenz & Lal, 2014). However, the influence of trees on soil health may differ for different tree species, and understanding this is crucial for designing effective restoration strategies. Insights can be gained from the field of functional ecology (Laughlin, 2014; Sandel, Corbin, & Krupa, 2011), which provides a framework to mechanistically link land use with species' functional traits and ecosystem function (e.g. Cadotte, Carscadden, & Mirotnick, 2011; Díaz et al., 2007; Lavorel et al., 2010).

Plant functional traits, and at a coarse biological scale functional types, are indicators of plant strategies and of how species influence ecosystem function (Petchev & Gaston, 2006). Accordingly, many

plant functional traits and types contribute to soil health (Table 1). Wood density, for instance, indicates species' positioning along the "resource-economics spectrum" (Chave et al., 2009). High-wood density species have expensive-to-construct tissues that decompose slowly, and thereby have a more constant and lasting positive effect on SOC inputs (de Deyn, Cornelissen, & Bardgett, 2008). Functional traits that describe the architecture of trees may influence soil health by altered understorey climatic conditions. For instance, trees that have a tall and narrow growth form will shade the soil to a lesser extent and may increase temperature, decrease soil moisture and negatively affect soil health (Chapin, 2003; Lin et al., 2016). Furthermore, certain functional types are known to have specific effects on soil health. Trees able to fix atmospheric dinitrogen (N_2) do so by mutualistic symbiosis with bacteria, resulting in faster growth (Batterman et al., 2013) and enhanced soil health (e.g. Adams, Turnbull, Sprent, & Buchmann, 2016; Bradford et al., 2002). Deciduous species undergo leaf senescence for part of the year, thereby producing large quantities of litter for organic-carbon inputs into the soil (de Deyn et al., 2008). In contrast, some functional types are known for their negative impacts on soil health: invasive species have been associated with increased erosion (Grover & Musick, 1990; Vågen & Winowiecki, 2014), decreased ecosystem carbon (Jackson, Banner, Jobbágy, Pockman, & Wall, 2002) and decreased streamflow (Cleverly, Smith, Sala, & Devitt, 1997). Also commonly planted exotics such as *Eucalyptus* spp. may reduce understorey vegetation cover and diversity (Thijs et al., 2014) and negatively impact hydrology (Zhou, Morris, Yan, Yu, & Peng, 2002; but see Reynolds, Wassie, Wubalem, Liang, & Collins, 2016).

Besides predictions on how species-level functional traits and types influence ecosystem function, two main theories explain how the traits of species co-occurring in a community (community-level functional properties) influence ecosystem function. The mass-ratio hypothesis predicts that the traits of the dominant species drive functions (Grime, 1998), while the niche complementarity hypothesis predicts that functionally diverse communities are better able to make optimal use of available resources and thereby increase overall functionality (e.g. Cardinale et al., 2012).

We evaluate the extent to which vegetation contributes to soil health. We do so by assessing a hierarchy of vegetation indicators that reflect increasingly detailed characteristics of the vegetation and thereby systematically assess what aspects of vegetation should be promoted for restoring degraded landscapes.

TABLE 1 Summary of the hypothesized relationships between functional traits/types and soil health. +/- indicate positive/negative predicted effects on soil health, indicated by SOC (soil organic carbon) (positively) and erosion (negatively)

Functional trait/ type	Plant strategies and ecosystem function	Effect on soil health
Wood density	Conservative strategy, slow growth, slow decomposition, above-ground biomass	+
Adult height	Light demanding, more evapotranspiration, above-ground biomass, tall architecture causing less shading	-
N_2 -fixing	Fast growth, high foliar nitrogen, N-mineralization, soil nitrification	+
Deciduous	Less evapotranspiration, faster decomposition, more litter production, shallow roots, high wood density	+
Invasive	Out-competing original vegetation cover, fast growth and reproduction	-
Exotic	Fast growth, light demanding, reduced soil water availability	-

We hypothesize that: (i) increased vegetation cover reduces soil degradation (increases SOC and decreases erosion); (ii) above-ground woody biomass reduces soil degradation; and (iii) functional properties of the vegetation affect soil degradation. Specifically, (a) increased functional diversity (FD) reduces soil degradation, (b) particular functional traits (high wood density, low adult height) reduce soil degradation, and (c) particular functional types of woody vegetation (N_2 -fixers, deciduous species) reduce soil degradation while other functional types (invasive species, exotic species) increase soil degradation.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study took place in five agricultural landscapes in three countries in East Africa (Figure 1). All landscapes are characterized by smallholder farming systems and are degraded, indicated by widespread erosion. Table S1 summarizes key climatic variables and vegetation types per landscape, while Figure S1 gives the variation in vegetation structure found across landscapes.

In Uganda, we focused on two landscapes in eastern Uganda, bordering Mount Elgon National Park: Mbale (34.24E, 1.09N) and Bumagabula (34.39E, 1.16N). The area is characterized by a mountainous topography, where Bumagabula is located at higher elevation and has higher rainfall than Mbale. Maize, legumes, banana and coffee are commonly cultivated, often in agroforestry systems, with some eucalypt plantations and cattle grazing areas. The region has high population densities, estimated at 620 persons per km^2 in 2002 (UBS,

2012). In Ethiopia, we focused on two landscapes, the subhumid Ano (36.97E, 9.09N) and the semi-arid Alem Tena (38.90E, 8.24N). In both sites, the main crops were sorghum, maize and teff, with trees commonly integrated into farming systems (liyama et al., 2016). In Kenya, we focused on one landscape, Waita (38.19E, 0.91S), in Kitui county. This is a lowland site where smallholder farmers cultivate maize, millet and sorghum with small-scale cattle production. Waita is the driest of our landscapes with an annual rainfall of 767 mm per year.

2.2 | Sampling framework

The Land Degradation Surveillance Framework (LDSF) was used to assess biophysical indicators at the five landscape sites. The LDSF uses a hierarchical sampling framework; each site is 100 km^2 , and consists of sixteen 1- km^2 clusters, each cluster consists of ten 1,000- m^2 sampling plots and each plot consists of four 100- m^2 subplots (Vågen, Winowiecki, Tamene Desta, & Tondoh, 2013). Positioning of sites was based on ongoing project activities in areas of interest. Locations were randomized to cover variation in topography and land uses while avoiding lakes and rivers. The LDSF is designed for simultaneously assessing key indicators of ecosystem health across multiple spatial scales and at geo-referenced locations.

2.3 | Soil health indicators

Soil erosion prevalence was scored at each subplot ($n = 640$ observations per site), when erosion was observed in over half of the four subplots per plot, this plot was considered to be severely eroded (binary 0/1). Topsoil samples (0–20 cm) were collected at each subplot and



FIGURE 1 Maps of the five study locations across three countries in East Africa. See Table S1 and methods for more information

thoroughly mixed to form a composite topsoil sample for each plot. SOC and sand content were measured through MIR absorbance, detailed methods of which are presented in Appendix S1. Mid-infrared spectroscopy is becoming a well-established method for predicting soil properties (cf. Madari et al., 2006; Reeves, Follett, McCarty, & Kimble, 2006; Vågen, Winowiecki, Abegaz, et al., 2013). Ten percent of the soil samples collected at each site were considered reference samples ($n = 32$ per site) and were analysed for SOC and sand content. Calibration models were developed for the prediction of soil properties using MIR spectra from the ICRAF pan-African MIR spectral library and the results of soil analysis on the reference samples (Vågen, Winowiecki, Abegaz, et al., 2013; Vågen, Winowiecki, Tondoh, Desta, & Gumbricht, 2016). This method has been shown to accurately predict SOC across Sub-Saharan Africa (Vågen et al., 2016).

2.4 | Vegetation cover and biomass estimations

Vegetation covering the soil (mainly herbs and grasses) was rated in each of the subplots using a Braun–Blanquet vegetation rating scale that ranges from 0 (exposed soil) to 5 (>65% cover; Braun-Blanquet, 1932). Plot-level vegetation cover represents the mean of the vegetation cover classes from the four subplots. Tree inventories were carried out in slightly different ways depending on the site, as explained in detail in Appendix S2. We estimated plot-level above-ground biomass (Mg/ha) using a generic allometric formula based on the diameter at breast height (DBH), species-specific wood density and a site-specific “environmental stress factor” (Chave et al., 2014). This was expressed on a per-hectare basis as and is thus corrected for differences in plot-level sampling effort across the sites and plots.

2.5 | Functional properties of the woody vegetation

A total of 2,673 trees belonging to 137 different species were identified across the five landscapes. Data for a number of relevant functional traits and types were retrieved from floras and online sources for the tree species: Wood density (g/cm^3), adult height (m), N_2 -fixing (0/1), deciduous (0/1), invasive (0/1) and exotic (0/1), for which detailed methods are presented in Appendix S3.

Species-level functional traits were scaled to plot-level functional properties using two complementary metrics: community-weighted mean (CWM) and FD. The CWM (Garnier et al., 2004) is calculated based on each single trait or type and weighted by species' relative basal area in the plot. For continuous trait values, the CWM reflects the trait value of “the weighted-average woody plant” in the community, for binary variables this reflects the proportion of the basal area that is represented by that type. FD was calculated using Rao's quadratic entropy (Rao's Q) (Botta-Dukát, 2005) and is based on the functional distance between species weighted by their relative basal areas, making use of all traits simultaneously. Rao's Q is conceptually similar to functional dispersion (Laliberté & Legendre, 2010) and estimates how functionally different the co-occurring species are. Plot-level functional properties were calculated using the R package “FD” (Laliberté & Shipley, 2012).

2.6 | Statistical analysis

In this study, we took the plot as a unit of replication, with a total of 745 plots. We used generalized linear mixed models, from the R package “lme4” (Bates, Maechler, Bolker, & Walker, 2015) to systematically test for the effects of vegetation on soil health in a series of models that reflect increased complexity (Table 2).

Mixed-effects models enable accounting for differences in cross-site sampling design, by taking site as a random effect, allowing a random intercept for each site. With package “LMERConvenienceFunctions” (Tremblay & Ransijn, 2015), we confirmed that site indeed contributed as a random effect. In model 5, we systematically replaced the different plot-level functional properties ($6 \text{ CWM} + 1 \text{ FD} = 7$ variations on model 5), resulting in 12 models per soil health indicator and 24 models in total.

The model with the best fit was selected based on Akaike information criterion, adjusted for small sampling size (AIC_c) (Burnham & Anderson, 2002). AIC penalizes for model complexity, hence taking a conservative approach to assessing the impacts of trees and functional traits on soil health. When models did not differ significantly ($\Delta\text{AIC}_c < 2$), we chose the model that had the highest marginal and conditional R^2 (Nakagawa, Schielzeth, & O'Hara, 2013), computed using package “piecewiseSEM” (Lefcheck, 2015). For severe erosion (binary, 0/1), we used glmer (family = binomial) while for SOC (continuous, range 3–96 g/kg) we used lmer. Model statistics were derived using packages “sjstats” and “sjPlot” (Lüdtke, 2016a, 2016b), while significance levels reflect the z-associated p -value (for erosion), or the t -associated p -value (for SOC) derived using “nlme” (Pinheiro, Bates, DebRoy, & Sarkar, 2016). All analyses were carried out using R version 3.2.4 (R Core Team, 2014).

3 | RESULTS

3.1 | Site conditions

The five East African study sites represent a large variety of climatic, topographical and land-use characteristics (Figures S1 and S2). Erosion was widespread across the sites (67%–99% across each landscape), indicating the need for more sustainable land management practices and land restoration activities. Average topsoil OC was $29.8 \text{ g}/\text{kg} \pm 13.2$ for Bumagabula, $27.9 \text{ g}/\text{kg} \pm 4.2$ for Ano, $21.2 \text{ g}/\text{kg} \pm 8.3$ for Mbale, $14.3 \text{ g}/\text{kg} \pm 4.0$ for Alem and $10.1 \text{ g}/\text{kg} \pm 4.0$ for Waita (Figure S2).

3.2 | Optimal model

The most complex model, with the largest number of variables (Table 2, model 5), best explained SOC and soil erosion. This model included soil texture (sand content), vegetation cover, above-ground woody biomass and functional properties of the woody vegetation. We found that soil health (lower erosion and higher SOC) was associated with higher vegetation cover and higher above-ground biomass, as expected. After controlling for these, we found that distinct functional properties related to distinct aspects of soil health; invasive species were associated with increased erosion while FD was associated with increased SOC (Figures 2 and 3, Table 3). Although our

TABLE 2 The models tested in this study that reflect increasingly detailed information on the vegetation to explain soil health (erosion and SOC (soil organic carbon)). Given are the rationale for each model and the implications for restoration

#	Model	Rationale	Implications for restoration
1	Soil health ~ Intercept	Data cannot explain soil health	None
2	Soil health ~ Sand content	Soil texture explains soil health	None
3	Soil health ~ Sand content + Vegetation cover	Vegetation cover contributes to soil health	Promote vegetation cover
4	Soil health ~ Sand content + Vegetation cover + Above-ground woody biomass	Above-ground biomass contributes to soil health	Plant and promote trees
5	Soil health ~ Sand content + Vegetation cover + Above-ground woody biomass + Functional properties (CWM/FD)	Functional properties contribute to soil health	See 5a and 5b
5a	Soil health ~ Sand content + Vegetation cover + Above-ground woody biomass + Community-weighted mean functional-trait values ^a	Functional traits of the dominant species contribute to soil health (mass-ratio effect)	Plant and promote specific functional types of trees (and avoid others)
5b	Soil health ~ Sand content + Vegetation cover + Above-ground woody biomass + Functional-trait diversity	Functional diversity contributes to soil health (niche complementarity effect)	Plant and promote a diverse range of functional types of trees

^aCWMs are calculated for single traits, so this model was tested for each of the six functional traits and types, see Table 1 for specific hypotheses.

model selection suggests a role for functional properties of the woody vegetation in explaining soil health, their marginal effects alone were not significant. The variance explained by the total model for severe erosion was 40% (32% for fixed factors alone), while the variance explained for SOC was 56% (11% for fixed factors alone). Model fit did not improve when allowing the sites to differ in the vegetation indicators' fixed factor effects, suggesting that the effects found are consistent across the sites. Table S2 gives the intercepts across the sites.

4 | DISCUSSION

Restoration of agricultural landscapes provides an opportunity to increase the productivity and resilience of agricultural systems and simultaneously contribute to conservation objectives. Functional ecology is

a promising tool to guide science-based restoration (Laughlin, 2014) though its application to managed agricultural landscapes has been lagging (Wood et al., 2015). In this study, we applied a trait-based approach to soil health in degraded agricultural landscapes and found that the marginal effects of the vegetation and their functional properties were directionally intuitive and had clear implications for restoration.

4.1 | Vegetation effects on soil health

We found that vegetation cover and above-ground biomass are important for soil health as higher values were associated with increased SOC and decreased erosion. We also found marginal additional effects for the functional properties of the woody vegetation. Invasive species were associated with increased erosion, while FD was associated with increased SOC.

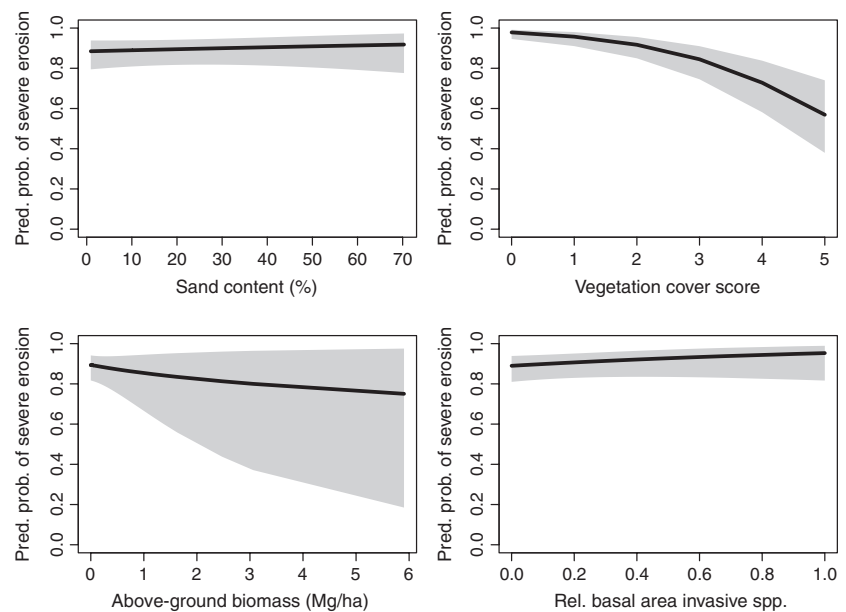


FIGURE 2 Marginal effects of fixed effects predicting the probability of encountering severe erosion

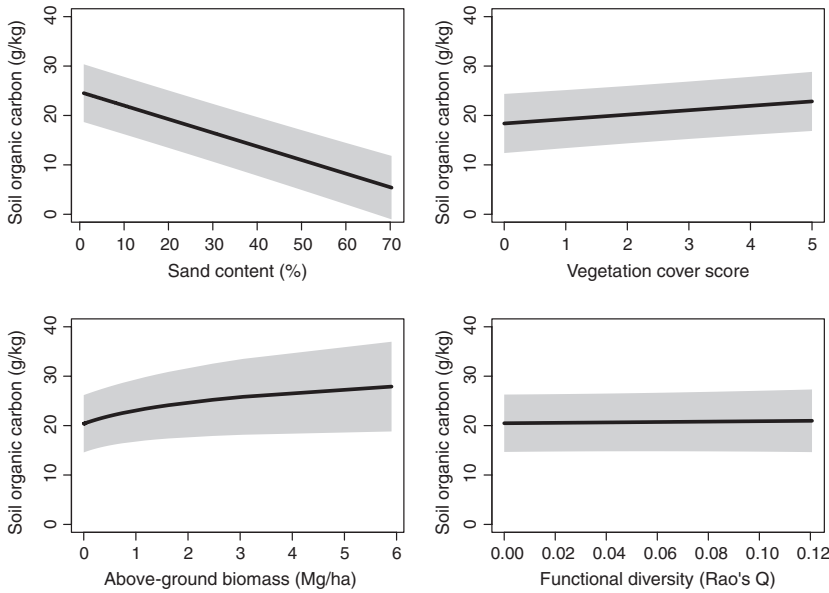


FIGURE 3 Marginal effects of fixed effects predicting soil organic carbon

TABLE 3 Fixed-effects statistics for the optimal models explaining soil health: (a) severe erosion prevalence and (b) SOC (soil organic carbon). Given are the beta estimates, the odds ratio and associated confidence intervals (for erosion) or standardized beta estimate and associated confidence intervals (for SOC). *p*-values reflect the *z*-associated *p*-value (for erosion), or the *t*-associated *p*-value (for SOC). Site (# = 5) was included as a random effect for all models, total *N* = 745

(a) Severe erosion ($R^2_{\text{conditional}} 0.40, R^2_{\text{marginal}} 0.32$)					
Predictor	Estimate	Odds ratio	CI	<i>p</i>	
Intercept	3.73	41.59	15.79 to 109.57	<.001	
Sand content	0.005	1.01	0.99 to 1.02	.546	
Vegetation cover	-0.708	0.49	0.39 to 0.62	<.001	
Above-ground biomass	-0.536	0.59	0.16 to 2.19	.427	
CWM invasives	0.919	2.51 ^a	0.62 to 10.13	.197	
(b) Soil organic carbon (SOC) ($R^2_{\text{conditional}} 0.56, R^2_{\text{marginal}} 0.11$)					
Predictor	Estimate	CI	Std. estimate	CI	<i>p</i>
Intercept	22.4	16.41 to 28.43			<.001
Sand content	-0.28	-0.33 to -0.23	-0.35	-0.42 to -0.29	<.001
Vegetation cover	0.89	0.32 to 1.47	0.17	0.06 to 0.28	.014
Above-ground biomass	3.89	0.22 to 7.57	0.05	0.00 to 0.10	.038
Rao's Q	4.12	-18.97 to 27.20	0.01	-0.04 to 0.06	.726

^aProbability of erosion under invasive species is then $(41.59 \times 2.51)/(1 + 41.59 \times 2.51) = 0.99$.

Our results substantiated that functional traits affect soil carbon (de Deyn et al., 2008) and erosion (Lorenz & Lal, 2005; Stokes, Atger, Bengough, Fourcaud, & Sidle, 2009). Our findings suggest that the mechanism by which the functional properties influence soil health depends on the indicator; we found that erosion resistance is driven by the traits of the dominant species (mass-ratio effect), while SOC was driven by the diversity of traits in the ecosystem (niche complementarity effect).

4.1.1 | Erosion

Above-ground vegetation quantity (cover and biomass) is directly related to below-ground vegetation quantity and, not surprisingly, root

quantity and distribution in the soil are of huge importance to prevent erosion (e.g. Durán Zuazo & Rodríguez Pleguezuelo, 2008; Gyssels, Poesen, Bochet, & Li, 2005; Stokes et al., 2009). There are large inter-specific differences in effects on soil stability (Berendse, van Ruijven, Jongejans, & Keesstra, 2015; Stokes et al., 2009), which may be driven by differences in species traits. We found that higher abundance of invasive species was associated with increased erosion, suggesting that the traits of the dominant species, and not the diversity, explain erosion. Increased erosion under invasive species has been repeatedly documented (Grover & Musick, 1990; Kourtev, Ehrenfeld, & Häggblom, 2002; Vågen & Winowiecki, 2014). Possible mechanisms include that invasive species tend to invest less in soil-stabilizing root

biomass compared with noninvasive species (van Kleunen, Weber, & Fischer, 2010) and that invasive species inhibit understorey vegetation cover. Although the effect of invasive species was by itself not statistically significant, the effects size suggested that an invaded site has a 99% chance to be severely eroded (Table 3). This is noteworthy given that invasive properties of a species, as found in the literature, reflect the species' potential to invade and not whether it is actually invading the site. Besides being a potential driver of degradation, invasive species can also be a symptom of degradation. Possible positive feedback mechanisms regarding invasive species and degradation could potentially lead to irreversible degradation if restoration efforts are not implemented in time. Our result confirms that decreasing the abundance of invasive species should be a priority in restoration efforts.

4.1.2 | Soil organic carbon

Soil carbon stocks result from the balance between carbon input via primary productivity and carbon output via decomposition, volatilization (e.g. by charring or burning), leaching and erosion of topsoil (Amundson, 2001). We found that vegetation cover and biomass increased SOC. Indeed, cover and biomass reduce erosion, as discussed in the previous section. Above-ground biomass is a driver of primary productivity (Lohbeck et al., 2015), although it may also accelerate decomposition by enhancing soil moisture by reducing evaporation (Lebrija-Trejos, Pérez-García, Meave, Poorter, & Bongers, 2011). Further, more biomass generally produces more litter (Lohbeck et al., 2015), providing a primary input for SOC. We also found an effect of FD on SOC, suggesting that resource-use complementarity in a plant community, possibly in combination with facilitation, enhances SOC content. Previous research similarly reported the niche complementarity effect to be a major driver of SOC in experimental grasslands (Fornara & Tilman, 2008) and in agroforestry systems in India (Hombegowda et al., 2016). In contrast, a recent study in Chinese subtropical forest showed that SOC was mainly influenced by the community-weighted maximum height of the trees, and less by FD (Lin et al., 2016).

Consistent with functional ecology theory (Díaz et al., 2007), our results suggest that functional traits play a role in carbon dynamics by mediating species differences in productivity and decomposition. Empirical evidence supports that niche complementarity drives primary productivity in tropical forest (Haggar & Ewel, 1997) as well as in temperate grasslands (Wilsey & Potvin, 2000). Other studies instead support the mass-ratio hypothesis showing that the functional traits of the dominant species drive productivity (Paquette & Messier, 2011; Warren, Topping, & James, 2009). Similarly for litter decomposition, studies have found both diversity effects (Finerty et al., 2016; Scherer-Lorenzen, 2008) and effects of the traits of dominant species on decomposition rates (Garnier et al., 2004; Tardif & Shipley, 2013). Probably both mechanisms matter for ecosystem function (Handa et al., 2014; Lohbeck et al., 2015). Our diversity-effect could indicate a direct diversity-effect of vegetation on SOC through productivity and decomposition (Hooper et al., 2005), but also an indirect effect

mediated by soil biota (Zak, Holmes, White, Peacock, & Tilman, 2003). This suggests that when farmers decide to plant trees on their fields, it is beneficial to choose species that are functionally complementary to the ones already established.

4.2 | Small marginal effects of functional properties

The variances explained by the fixed effects were quite small, particularly for erosion (R_m 0.11). High levels of severe erosion across our landscapes (67%–99%) reduced the variation in which vegetation-effects could be detected. Our alternative models were designed to reflect increasingly detailed aspects of the vegetation, taking a conservative approach to the marginal effects of functional properties, which partly explains why effects were small and statistically not significant (Table 3). It is important to recognize that this observational study represents a large variation of landscapes shaped by different people and land management practices. There is a great need to test whether functional-trait effects on soil functions can be detected in dynamic human-modified landscapes, and what the implications are for restoration, which is what we explored in this study. Although the marginal effects of functional properties are small, we consider our findings important because functional properties of the vegetation can easily be modified by selecting species with suitable functional traits when planting trees on farmland. This approach, thus, contributes to a much-needed evidence-base for restoring agricultural landscapes.

4.3 | Synthesis and applications

Based on our findings, we are able to draw recommendations that will advance the field of functional ecology in managed agricultural landscapes. We showed that (nonwoody) vegetation cover strongly influenced soil properties, suggesting that including functional traits of nonwoody vegetation will increase our understanding of trait-mediated effects of vegetation on soils. Besides the direct effects that plants exert on soil functions, there are some important indirect linkages between plants and the soil, mediated through management, symbionts and soil biota. Management practices, such as tillage, the use of fire and fertilizers, were not included in our analyses. Management directly affects soil function but also indirectly through the vegetation. We were constrained to functional traits available from online sources and floras, which is a limited subset of above-ground traits and limited to woody vegetation. Below-ground plant traits (related to root biomass and turnover) are of particular importance for soil functions (McCormack et al., 2015; Prieto, Stokes, & Roumet, 2016; Schroth, 1995). Future research on functional ecology in agricultural landscapes will need to include traits of nonwoody and cultivated species, and more explicitly include the direct and indirect effects of management on plant communities and on soil health.

Understanding the functional ecology of managed systems is an important step towards making informed decisions on restoration planning, both at the plot-level and at landscape-scale. Applying this approach to degraded East African landscapes, we suggest that in addition to avoiding exposed soil and promoting trees on farms, priority

should be given to the removal of invasive species and promotion of higher FD of trees on farms for restoring important soil functions such as SOC and increased resistance to erosion.

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AUTHORS' CONTRIBUTIONS

M.L., T.-G.V. and L.W. conceived the ideas and designed the methodology. M.L., T.-G.V., L.W., E.A. and C.O. collected the data. M.L., T.-G.V., L.W. analysed the data, M.L. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

LDSF sites data are available from Harvard Dataverse: Ethiopia: <https://doi.org/10.7910/dvn/29652> (Aynekulu & Shepherd, 2015), Kenya: <https://doi.org/10.7910/dvn/sbl270> (Winowiecki & Sinclair, 2016), Uganda: <https://doi.org/10.7910/dvn/eqfm2n> (Vågen et al., 2017).

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SUPPORTING INFORMATION

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