



Diversity and composition of agroforestry species in two agro-ecological zones of Rwanda

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Abstract This study delves into the diversity and composition of agroforestry species in Rwanda's Eastern Plateau and Eastern Savannah agro-ecological zones. Examining these systems across diverse landscapes is crucial for selecting species adapted to local conditions. We surveyed four landscapes with varying tree cover levels, using stratified random sampling to allocate 240 plots for detailed field inventory. We analyzed dendrometric characteristics of woody vegetation, focusing on plants with ≥ 4 cm

diameter at breast height (DBH). Exotic tree species comprised over 75% of trees across all landscapes. Diversity indices indicated significant differences in plant communities between the Eastern Savannah and Eastern Plateau, with higher diversity in the former. Sørensen's similarity coefficient for woody species between the two regions showed a moderate level of similarity (approximately 53%). However, there was a significant difference in the equitability of on-farm tree species between the zones, suggesting non-identical distribution patterns. The most common and dominant tree species were *Grevillea robusta*, *Mangifera indica*, and *Persea americana*, primarily

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used for timber and fruit production. Most encountered trees were small and scattered, with nearly 80% having a DBH below 20 cm, highlighting the prevalence of young trees. The dominance of exotic species emphasizes the need for further research on their impact on agricultural biodiversity, informing sustainable land management practices in Rwanda and similar contexts.

Keywords Agroforestry systems · Biodiversity · Forest · Landscapes · Land use · Woody vegetation structure

Introduction

Over centuries, agricultural expansion and timber extraction have dramatically devastated natural ecosystems, causing significant biodiversity loss globally (Foley et al. 2005; Sallustio et al. 2018). This landscape transformation, driven by human actions like land-use changes for intensive agriculture, disrupts landscape ecological processes. For instance, these alterations, altering slopes, soil, and vegetation, accelerate soil erosion, which further exacerbates natural degradation, impacting food security and ecosystem functioning (Mohamad et al. 2020). Therefore, agricultural landscapes sprawl across vast expanses (Taylor and Rising 2021), requiring a nuanced assessment of the diversity, structure and composition across various agricultural landscapes, representing different levels of tree cover. This is essential for understanding the underlying effects of land use and distribution of tree legacy across diverse agroecological regions (Anwar et al. 2023; Petsch et al. 2021; Roy et al. 2022).

The vulnerability of tree-poor landscapes undermines agricultural resilience, exacerbating global environmental challenges (Foley et al. 2005; Tscharncke et al. 2011). Amidst these challenges, agroforestry emerges as a promising approach, offering multifaceted solutions to climate change and biodiversity loss (Barrios et al. 2018; Fargione et al. 2018). Recognized by institutions like the FAO and ICRAF, agroforestry epitomizes a nature-based solution, addressing the complex needs of agricultural systems (FAO 2015; Ji and Lee 2021; Zinngrebe et al. 2020).

A widely used scheme for describing the role of trees on farms and in farming landscapes define

“Agroforestry” as a collective name for land-use systems and technologies where woody perennials (trees, shrubs, palms, bamboos, etc.) are deliberately used on the same land management unit as agricultural crops and/or animals, in some form of spatial arrangement or temporal sequence (Sinclair 1999). In agroforestry systems there are both ecological and economic interactions between the different components (Kohli et al. 2008; Murthy et al. 2017). Due to its potential to landscapes resilience, agroforestry is depicted as the future of land use (van Noordwijk et al. 2019; Swift et al. 2004).

Rwanda’s agroecological zones, particularly in the eastern Savannah and plateau regions, face rapid land use changes and climate impacts, leading to soil degradation (Rushemuka et al. 2014). Farming practices, climate conditions, and poverty exacerbate the decline of trees in these regions (Bucagu et al. 2013; Verdoodt and Van Ranst 2006). Despite their position within the relatively low topographic landscape of Rwanda, this region stands out as the most severely affected by soil degradation throughout the country (Nambajimana et al. 2019). Over the decades, the Eastern Province, has witnessed dramatic declines in woody Savannah land. This conversion is particularly evident in Umutara and Bugesera, where woody Savannah land has shrunk dramatically (SANBI 2022). For instance, in 1983, there were over 50,000 ha recorded, but by 1988, this figure had plummeted to less than 10,000 ha (MINAGRI 1988). Consequently, this has markedly heightened the region’s susceptibility to the adverse effects of soil degradation (Rushemuka et al. 2014). Despite afforestation efforts in Rwanda in the last two decades, deforestation rates exceed afforestation rates in the Eastern Province, underscoring the urgent need for restoration efforts in the eastern Savannah and eastern plateau to mitigate the consequences associated with the lack of forests in these agroecological zones (MoE 2019). A greater understanding of what drives habitat loss within each ecosystem type of this region is critical to understand, as highlighted by the first national and recent spatial biodiversity assessment (SANBI 2022). Here, we explored whether the distribution of woody vegetation in agricultural landscapes might be agroecological zones-specific, which is explained by differences in farming systems, climate condition, the altitude and soil characteristics (Delepiere 1982).

We selected four distinct farmlands within the eastern plateau and eastern Savannah agroecological zones of Rwanda. Through a comparative analysis

of these farmlands, our aim was to identify the relationship between trees on farms, farmland types, and agroecological zones enhancing our understanding of the diversity, structure, composition, and demographic structure of agroforestry species within these zones. The following questions guided this research:

- (i) How does the species composition and diversity of agroforestry species differ between the eastern Savannah and eastern plateau agroecological zones of Rwanda?
- (ii) What are the structural characteristics of agroforestry species across the two agroecological zones?
- (iii) What is the demographic structure of agroforestry species in the two agroecological zones?

We hypothesized that within the eastern plateau and eastern Savannah agroecological zones, there exists a positive correlation between on-farm tree diversity and composition and decreasing forest cover in the surrounding landscape. This correlation is likely influenced by human behaviour, specifically farmers strategically planting trees on their farms to supplement or replace access to wood and non-timber forest products (NTFPs) traditionally obtained from natural ecosystems and forest plantations. This paper is a baseline for exploring agroforestry practices in Rwanda's agroecological zones within the context of landscape dynamics and human interactions.

Methods

Study sites

Our study investigates tropical agricultural landscapes in Rwanda, geographically located in Central Africa between 1°04' and 2°51'S and between 28°45' and 31°15'E (Fig. 1). We examine four distinct landscape sites located in two agroecological zones: the Eastern Plateau and the East Savannah. These zones are characterized by differences in altitude, rainfall, and soil properties and encompass a range of macroclimatic conditions (Delepiere 1982; Table 1) and land cover types (Table 2), each contributing uniquely to the ecological makeup of their respective zones. In the Eastern Plateau and Eastern Savannah agroecological zones, which encompass the lowlands of Rwanda, temperatures soar to higher levels compared to other regions of the country. In February

and July–August, temperatures can surpass 30 °C, nearly doubling the average annual temperature range for Rwanda, which typically falls between 16 °C and 20 °C (MINIRENA 2011). Conversely, regions such as the high areas of the Congo-Nile ridge boast milder climates, with average temperatures ranging from 15 °C to 17 °C and abundant rainfall. The volcanic region experiences even lower temperatures, occasionally dropping below 0 °C in certain locales (MINIRENA 2011). Intermediate altitude areas maintain average temperatures ranging from 19 °C to 21 °C, with an average annual rainfall of around 1000 mm (World Bank Group, 2022). Despite this, rainfall in these regions can be less consistent, leading to occasional drought periods. Notably, the Eastern Plateau and Eastern Savannah agroecological zones face more pronounced thermic challenges compared to the rest of the country, with rainfall ranging from 700 to 970 mm per year. Therefore, we intentionally selected two distinct landscapes per agroecological zone to ensure coverage of diverse environmental characteristics and to maximize the efficiency of hypothesis testing.

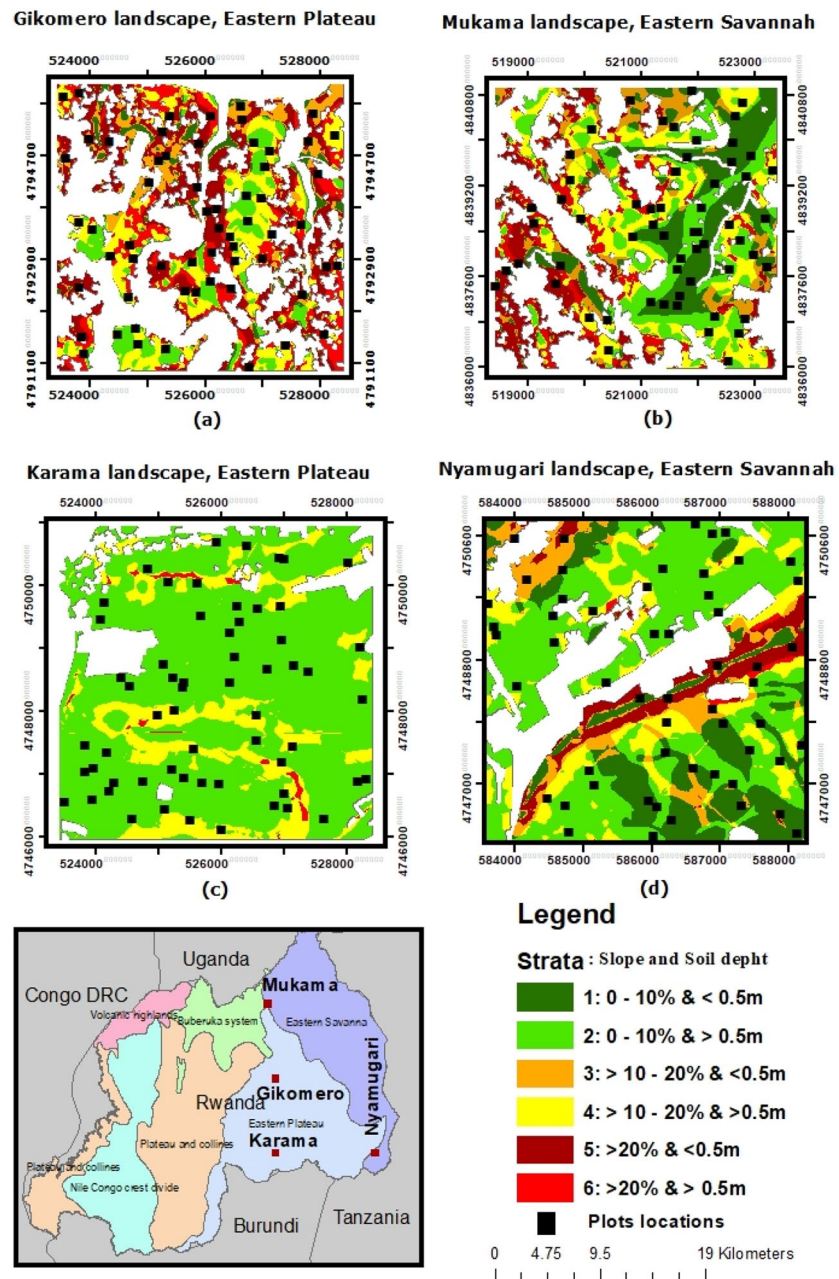
Land use types

We mapped land cover types within each of the selected landscapes using ArcGIS 10.8.2. Our analysis identified six primary land cover categories across the four landscapes: hill agriculture land, rural settlements, bare land/rock outcrops, water bodies, forest, and non-rice agricultural wetlands. Hill agriculture land dominates the landscapes in the study region, comprising 81.5% of the total area. Various types of forest follow closely, accounting for 11.1%. These forests include both state forests and community woodlots predominantly composed of eucalyptus species. Rural settlements constitute 5.5% of the total cover. Other land cover types, including water bodies, non-agricultural wetlands, and bare land/rock outcrops, each occupy less than 1% of the area and were therefore excluded from further analysis as explanatory variables for agroforestry species distribution across the two agroecological zones.

Sample plots and sampling methods

We used a landscape grid of 5 km×5 km windows overlaid with the land cover map to identify and select four representative landscapes (Table 2). To determine the potential

Fig. 1 Map of Rwanda showing the location of the four studied landscapes selected in the two agroecological zones of the eastern Rwanda. The four panels represent the four landscapes (5 km × 5 km window, each) and show six strata based on slope and soil depth. Six slope and soil-depth strata were identified: (a) Gikomero landscape in the eastern plateau, (b) Mukama landscape in the eastern Savannah, (c) Karama landscape in the Eastern Plateau and (d) Nyamugari landscape in the east Savannah. Sample plot locations in each stratum for each landscape are indicated by black dots



hillside agroforestry areas within each landscape, we employed a land use land cover classification based on the National Statistics of Rwanda classifications (Supplementary Information Table 1). This classification was generated by combining various geographical layers available for the country, along with a photo interpretation of high-resolution satellite images from Worldview (NISR 2021). To effectively stratify the landscapes, we applied

the landscape suitability criteria proposed by Verdoort and Van Ranst (2006), focusing specifically on soil depth and slope gradient. Slope gradients were categorized into three percentage ranges: 0–10%; >10–20%; and >20%. Soil depths were simplified into shallow (<0.5 m) and deeper (>0.5 m) categories. The plot size was meticulously selected to strike a balance between the necessity for detailed observation within each plot and the financial

Table 1 Regional characteristics of Eastern Savannah and Plateau Agroecological Zones classified into four categories of explanatory variables. [Source: Djimde 1988; Ndoli et al. 2021, if not otherwise specified with a superscript letter]

Set	Characteristics	Eastern Savannah	Eastern Plateau
Biophysical	Elevation (m)	1200–1400	1200–1500
	Rainfall (mm year ⁻¹)	800–1000	800–1000
	Temperature (°C)	> 21	20–21
Soil compositions	Proportion of very fertile soil (%)	48	54
Agricultural practices	Dominant agroforestry systems	Trees on-farm boundaries	Scattered trees on farm, trees on contour
	Tree species dominant in the surveyed landscapes	<i>Grevillea robusta</i> , <i>Mangifera indica</i> , <i>Persea americana</i> , <i>Ficus thonningii</i> , <i>Carica papaya</i>	<i>Grevillea robusta</i> , <i>Persea americana</i> , <i>Mangifera indica</i> , <i>Euphorbia tirucalii</i> , <i>Markhamia lutea</i>
	Livelihood	Agropastoral	Banana, cassava and mixed agriculture
Landscape structure	Network cover (%) of trees on farmland ^a	17.25	20.45
	Forest cover ^b (%)	17.9	23.2

^a (Mugabowindekwe et al. 2022)^b (NISR 2021)

resources available for the inventory. Deliberately, we opted for a plot size of 51 × 51 m (approximately 0.26 ha). This choice aligns with the minimum threshold utilized in the recent national forest cover assessment (MoE 2019). In that study, forested areas and shrublands of 0.25-hectare were excluded to focus on areas that had undergone deforestation, reforestation, or exhibited no change in forest cover. Additionally, the 0.25 ha area corresponds to half the average farm size in the study region (0.5 ha) (NISR 2021), rendering the plot size pertinent to the agroforestry inventory in the eastern Savannah and plateau agroecological zones of Rwanda. Subsequently, using a stratified random sampling tool procedure, interspaced by 200 m to

avoid collinearity of the plots, we allocated 60 plots proportionally to the sizes of each stratum, resulting in a total of 240 sampling plots across the four landscapes (Table 3). This approach enabled us to calculate the average for the entire survey area as the mean of all sample plots.

Quantifying landscape metrics

To quantify landscape metrics within each landscape study sites, we employed FRAGSTAT software version 4.2.1 (McGarigal et al. 2023). Land use percentages were previously calculated in ArcGIS based on field boundaries. FRAGSTAT analysis generated

Table 2 Land use types (in ha) and their proportions (in percentages) enclosed in brackets for the four landscape study sites within the Eastern Plateau and Eastern Savannah agroecological zones in Rwanda. [Source: NISR (2021)]

Code	Land use type	Eastern Plateau		Eastern Savannah		Overall
		Gikomero landscape	Karama landscape	Mukama landscape	Nyamugari landscape	
11	Hillside agricultural land	1780.6 (71.2)	2281.2 (91.2)	1976.1 (79.0)	2114.6 (84.6)	8152.6 (81.5)
4	Rural settlements	146.7 (5.8)	105.1 (4.2)	59.9 (2.4)	236.2 (9.4)	548.0 (5.5)
5	Bare land/rocks	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	56.6 (2.2)	56.7 (0.2)
6	Water bodies	54.4 (2.1)	7.2 (0.3)	0.0 (0.0)	88.1 (3.5)	61.6 (0.6)
9	Forest plantations	474.4 (18.9)	106.5 (4.3)	443.6 (17.7)	4.5 (0.2)	1112.9 (11.1)
21	Non-rice agricultural wetland	44.5 (1.7)	0.0 (0.0)	21.3 (0.8)	0.0 (0.0)	70.3 (0.7)

stratum-specific compositional metrics encompassing stratum size (i.e., Patch size) and percentage of on-farm tree cover. We selected these metrics based on their established influence on tree occurrence, and consequently, the diversity, composition and structural characteristics of agroforestry species within a specific agro-ecological farming system. All metrics were computed at the landscape level within each of the four landscape study sites. This analysis was conducted across six spatial strata. Compositional metrics (percentage tree cover in farmlands) were calculated based on remote sensing data obtained from (Mugabowindekwe et al. 2022). For comprehensive descriptions of all landscape metrics used, please refer to (McGarigal et al. 2023) (Fig. 2).

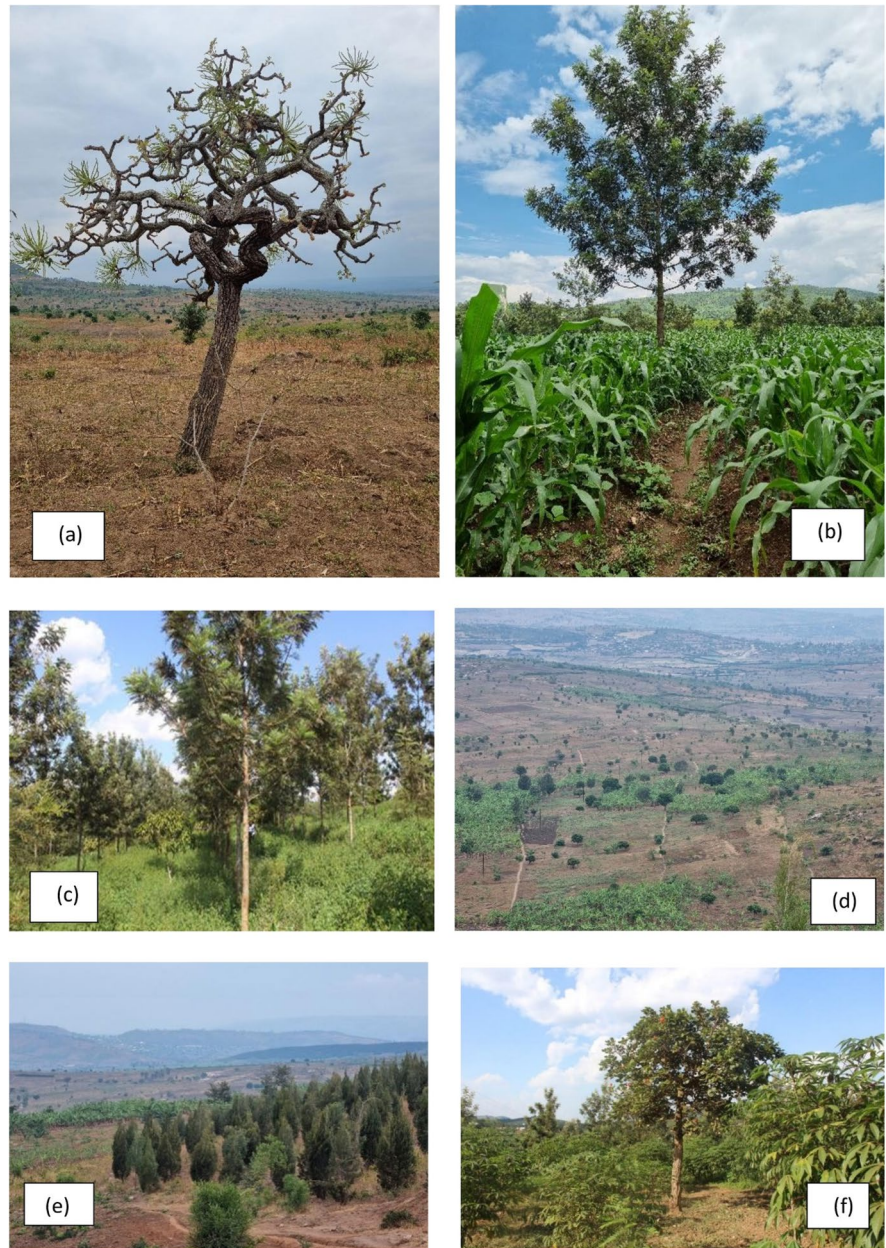
Landscape scale vegetation inventory

Agroforestry species inventory for this study was conducted from August to October 2021. The inventory resulted in a dataset of 221 plots, with a total of 1467 agroforestry species for the analysis. Plots that were found outside of the focal agroecological zones were omitted from the inventory. Thus, the final number of surveyed plots was less than the initial sample size (Table 3). We measured all woody plants with ≥ 4 cm diameter at breast height (DBH) following forest inventory methods; a threshold was set because measuring all individual small trees would be very time-consuming. In the field, basic plot characteristics that could help to explain the variability patterns between landscapes were observed. Plot-level information recorded included tree species and the spatial configuration of the trees within a plot (e.g., Mixed sparse, Boundary and trees in block). Individual tree structural properties, or ‘structural variables’ recorded included the diameter at breast height (DBH), height and crown diameter (e.g., average crown diameter for a long axis crown diameter and crown perpendicular axis diameter) in each sample plot. Stem diameter was measured at 1.30 m height for every tree having DBH > 4 cm in the sample plot using a aneol caliper and a diameter tape in centimeters. For multi-stemmed trees all the stems were counted and DBH were measured for the median tree. Tree height was determined using a Haga Altimeter. In the context of this study, a woody plant was defined as a tree and shrub that is wild/retained or was planted in the farmland (Table 4).

Table 3 Distribution of strata by slope percentage and soil depth across two agroecological zones: initial and final sample sizes (ss) in each stratum

Stratum	Description of strata	East Savannah			East Plateau			Total Area		Sample Sizes (SS)	
		Slope	Soil depth	Area (ha)	Proportion (%)	Initial	Final	Area (ha)	Proportion (%)	Initial	Final
1	0–10%		< 0.5 m	773	11	30	30	65	1	7	37
2	0–10%		> 0.5 m	1263	18	40	38	1926	28	40	80
3	> 10–20%		< 0.5 m	540	8	11	9	154	2	15	26
4	> 10–20%		> 0.5 m	455	7	22	19	679	10	28	50
5	> 20%		< 0.5 m	324	5	4	4	367	5	18	22
6	> 20%		> 0.5 m	156	2	13	1	242	4	12	25
Total	3511		51	120	101	3434	49	120	120	6945	221

Fig. 2 Examples of agroforestry systems in Eastern Savannah and eastern plateau of Rwanda. Note spatial arrangement of the woody component **(a)** Remnant and retained Savannah tree after conversion of forest to farmland; **(b)** Patches of corns and soybeans under an isolated exotic tree (*Grevillea robusta*); **(c)** Peas under trees (*G. robusta*) in rows – alley cropping on a conservation agricultural cropland; **(d)** Patches of banana plantation and scattered wooded trees in the farmland in the east Savannah; **(e)** Woodlots of exotic tree species (*Callitris carotrysis*) surrounded by farmland; **(f)** Patch of cassava under a native tree (*Erythrina abyssinica*). All pictures come from the studied landscapes in eastern province of Rwanda



Measuring agroforestry species diversity

We assessed on farm species diversity using richness (number of species) and diversity indexes (Shannon, Simpson, Evenness). These compare the ecological importance of different tree species across agroecological zones and how evenly distributed they are. The Shannon index, considering both abundance and richness, and is the most commonly

used index (Kent and Coker 1992). It is calculated for any sample as:

$$H' = -\sum p_i(\ln(p_i)) \quad (1)$$

where: H' = Shannon diversity indices; p_i equals the relative cover of the i th species.

In addition, the Simpson index (D) and the evenness index ($E = H'/H_{\max}$) are considered as a measure of species dominance and a measure for

Table 4 Estimates of the fractional species composition encountered in the four agricultural landscapes situated in two agroecological zones of Rwanda – the East Plateau and the East Savannah. RF: Relative Frequency (%); Rdo Relative Dominance Relative were used to provide the Importance value Index of encountered agroforestry species. The species were ranked in descending order of their overall frequency across the two zones

Species	Local name	Family	LF	W/P	N/E	Eastern Plateau		Eastern Savannah		Overall	Use
						(RF %)	(RDo%)	(RF %)	(RDo%)		
<i>Grevillea robusta</i> A.Cunn. ex R.Br.A.Cunn. ex R.Br	Gereveriya	Proteaceae	T	P	E	38.2	36.1	48.1	34.7	42.7	1,2,5,7,9,10,13,14,16,18
<i>Mangifera indica</i> L	Umwembe	Anacardiaceae	T	P	E	11	7.9	13.9	26	12.3	1,4,8,9,12,14,16,18
<i>Perseaanceolat</i> Mill	Avoka	Lauraceae	T	P	E	12.2	17.7	5.2	16.1	11	1,4,8,9,12,14,16,18
<i>Euphorbia tirucalli</i> L	Umuyenzi	Euphorbiaceae	S	P	N	14.1	11.3	7.4	2.3	9	9,11,12,18,19
<i>Carica papaya</i> L	Ipapayi	Caricaceae	S	P	E	2.4	2.3	8.8	6.1	5.5	4,8,12,14
<i>Markhamia lutea</i> (Benth.) K.Schum	Umusave	Bignoniaceae	T	P	N	7.4	3.8	3.1	2.3	5.3	1,4,9,10,13,14,16,18
<i>Eucalyptus saligna</i> Sm	Inturusu	Myrtaceae	T	P	E	2.5	2.2	5.8	2.5	4	1,3,5,9,10,12,16
<i>Ficus thonningii</i> Blume	Umuvumu	Moraceae	T	P	N	1.4	5.7	0.7	4.6	1.4	2,3,5,8,9,10,12,18
<i>Toona sinensis</i> (A.Juss.) M.Roem	Isederi	Meliaceae	S	P	E	1.8	2.3	0.9	0.8	1.3	5,7,9,14
<i>Ricinus communis</i> L	Ikibonobono	Euphorbiaceae	S	W	N	0.3	2.5			1.2	11,12,14,18
<i>Senna spectabilis</i> (DC.) H.S.Irwin and Barneby	Kasiya	Fabaceae	T	P	E	1.3	1			1.1	5,7,9,10,11,14,18
<i>Ziziphus abyssinica</i> Hochst. Ex A.Rich	Umukugutu	Rhamnaceae	T	W	N	0.1	2.6	0.4	0.3	0.8	12,18
<i>Jacaranda mimosifolia</i> D.Don	Jakaranda	Bignoniaceae	T	P	E	1.3	0.5	1.2	0.2	0.7	5,9,11,13,14,18
<i>Kigelia anceola</i> (Lam.) Benth	Umuvungavungo	Bignoniaceae	T	W	N	2.1	0.6	0.3	0.1	0.6	9,10,14,18
<i>Albizia petersiana</i> (Bolle) Oliv	Umumeyu	Fabaceae	T	W	N			0.3	1.2	0.4	1,3,9,10,13,14,18
<i>Dombeya torrida</i> subsp. <i>Torrida</i>	Umukore	Sterculiaceae	T	W	N			0.6	0.7	0.3	9,14,16,18
<i>Olea europaea</i> subsp. <i>Cuspidata</i> (Wall. And G.Don) Cif	Umunzenze	Oleaceae	T	W	N			0.1	1	0.3	1,3,9,10,13,14,18
<i>Gymnanthemum amygdalinum</i> (Delile) Sch.Bip	Umubirizi	Asteraceae	S	P	N	0.6	0.3	1	0.2	0.3	5,7,8,11,12,14,15,18,19
<i>Macademia ternifolia</i> F.Muell	Makadamiya	Proteaceae	T	P	E	0.5	0.4			0.3	4,8,12,19
<i>Citrus × limon</i> (L.) Osbeck	Indimu	Rutaceae	S	P	E	0.6	0.5	0.6	0.1	0.3	4,8,12,
<i>Markhamia obtusifolia</i> (Baker) Sprague	Umukundambazo	Bignoniaceae	T	W	N	0.1	0.6			0.1	1,2,3,9,13,15,,18
<i>Combretum pisoniflorum</i> (Klotzsch) Engl	Umurama	Combretaceae	T	W	N	0.6	0.6	0.1	0	0.1	9,10,
<i>Vachellia hockii</i> (De Wild.) Seigler and Ebinger	Umugenge	Fabaceae	T	W	N			0.3	0.3	0.1	12,15,18
<i>Osyris anceolata</i> Hochst. And Steud	Kabaruka	Santalaceae	S	W	N	0.1	0.4			0.1	12,19,
<i>Solanecio mannii</i> (Hook.f.) C.Jeffrey	Umutagara	Asteraceae	S	W	N	0.3	0.1	0.4	0.1	0.1	11,12,18,19
<i>Leucaena leucocephala</i> (Lam.) de Wit	Lesena	Fabaceae	S	P	E	0.5	0.1	0.1	0	0.1	8,9,18
<i>Vepris nobilis</i> (Delile) Mziray	Umuzo	Rutaceae	S	W	N			0.3	0.1	0.1	10,16
<i>Erythrina abyssinica</i> Lam	Umuko	Fabaceae	T	P	N	0.1	0.2			0.1	1,2,3,5,10,12,18

Table 4 (continued)

Species	Local name	Family	LF	W/P	N/E	Eastern Plateau	Eastern Savannah		Overall	Use
							(RF %)	(RDo%)		
<i>Psidium guajava</i> L.	Ipera	Myrtaceae	T	P	E	0.1	0.1		0.1	4,8,12
<i>Zanthoxylum chalybeum</i> Engl	Intare y'irungu	Salvadoraceae	T	W	N	0.1	0.1		0.1	12,14,15,18
<i>Senna didymobotrya</i> (Fresen.) H.S.Irwin and Barneby	Umucyuro	Fabaceae	S	W	N		0.1	0	0.1	1,10,12,18
<i>Spathodea campanulate</i> P.Beauv	Umunyara	Bignoniaceae	T	P	N	0.1	0	100	0.1	17,18
						100		100	100	100

Where, Local names: Kinyarwanda name; RF- Relative Frequency; LF- Life form: T -Tree, S- Shrub; T/S- Tree or shrub; Establishment methods: W-Wild, P- planted; State of the species: N-Native, E-exotic species;

Uses source: Woody plants of Rwanda: Flora, ecology and uses (Bloesch et al. 2009); Plants of the World Online | Kew Science and <https://tropical.theferns.info/>. 1: bee forage, 2:beehives construction, 3:beehives hanging, 4: cash, 5:farm tools, 6:flavouring drink, 7:fodder, 8:fruit/food, 9:Fuelwood and charcoal, 10:household's utensils, 11:live fences, 12: medicine, 13:Shade, 14:Soil fertility, 15:stimulus, 16:Timber/poles, 17:Ornamental, 18:Soil conservation, 19:Insecticide.

evenness of spread, respectively (Magurran 1988). Simpson index is defined as:

$$D = \sum P_i^2 \quad (2)$$

As biodiversity increases, the Simpson index decreases (ranging from 0 for infinite diversity to 1 for complete dominance by a single species). Therefore, the reciprocal (1-D) is often used (referred to as Simpson's Diversity Index) to get a clearer picture of species dominance.

Evenness (equitability index) was considered to assess the uniform distribution of tree species on farmlands. The evenness of tree species was calculated by:

$$E = \frac{H'}{H_{\max}} = \frac{H'}{\ln S} \quad (3)$$

With E=Evenness, H'=Calculated Shannon diversity, H max=ln(s) [species diversity under maximum equitability], S=Number of species. (where Hmax is the natural logarithm of the total number of species). This index ranges from 0 (uneven distribution) to 1 (perfect evenness).

The Sørensen coefficient of similarity (Ss) was used to calculate the species similarities of the species composition in the two agroecological zones. Sørensen coefficient of similarity (Ss) was defined by:

$$Ss = \frac{2a}{(2a + b + c)} * 100 \quad (4)$$

where, Ss=Sørensen similarity coefficient; a=number of species common to both samples; b=number of species in East Savannah; c=number of species in East Plateau.

Importance Value Index

We used the important value index (IVI) to assess the relative significance of individual tree species within agroforestry practices in the study region. The IVI was calculated for all species identified in the sampled plots by combining data for each species across all landscapes, following Eq. 9. Additionally, relative density, relative dominance, relative frequency, and absolute frequency were determined using Eqs. 5, 6, 7, and 8, respectively.

$$\text{Density} = \frac{\text{Total number of individual species}}{\text{Sample area (ha)}} * 100 \quad (5)$$

$$\text{Relative density} = \frac{\text{Density of individual of species}}{\text{Total density of all species}} * 100 \quad (6)$$

$$\text{Relative dominance} = \frac{\text{Total number of individual species}}{\text{Total number of species population}} * 100 \quad (7)$$

$$\text{Relative frequency} = \frac{\text{Frequency of a species}}{\text{Frequency of all species}} * 100 \quad (8)$$

$$\text{IVI} = \text{Relative density} + \text{Relative dominance} + \text{Relative frequency} \quad (9)$$

The basal area and crown projected area of tree species in the overall study sites and in two agroecological zones was calculated as follows:

$$\text{BA} = \frac{\pi}{4}(\text{DBH})^2 \quad (10)$$

where BA is the basal area (m^2) per tree, DBH is the diameter at breast height of the tree (in cm), π (pi) is a mathematical constant with a value of approximately 3.14

$$\text{CPA} = \frac{\pi}{4}(\text{CD})^2 \quad (11)$$

where CPA is the crown projected area (m^2), CD is the diameter at breast height of the tree (in cm), π (pi) is a mathematical constant with a value of approximately 3.14.

The stem density for a linear configuration was calculated using the following formula:

$$\text{Stem density} = \frac{\sum_{k=1}^n \text{BA}}{\pi \left(\frac{s}{2}\right)^2} * \text{Conversion factor} \quad (12)$$

where *Stem density* is stems per hectare, BA is the basal area of individual tree, spacing between trees (s) refers to the average distance between the centers of adjacent trees (in m), the conversion factor adjusts the units to stems per hectare, accounting for any necessary conversions. This converts the answer from square m to ha. A common conversion factor is 10,000 (as 1 hectare is equal to 10,000 square m).

Statistical analysis

All statistical analysis was performed using R software Version 4.3.2 (R Core Team 2023). The diversity indices were calculated using BiodiversityR package (Kindt and Coe 2018). We conducted the analysis of the structure of agroforestry species, examining the vegetation data at the tree level: diameter at breast height (DBH), height, and crown diameter. Additionally, plot-level dendrometric parameters such as stem density (trees ha^{-1}), basal area (per hectare), and crown projected area (per hectare) were assessed. These assessments were carried out across six strata within each agroecological zone. Normality of the dataset was evaluated using the Shapiro–Wilk test, with significance set at $p \geq 0.05$. Because our data were counts, to discern significant differences between landscapes, we employed the Kruskal–Wallis test at $p \leq 0.05$, a robust non-parametric method suitable for comparing multiple groups when the assumptions of ANOVA are not met. Pairwise comparisons between specific strata were then conducted using the Wilcoxon test, with adjustments made for multiple testing using the Bonferroni correction. The independent variables in our analysis included the six strata and spatial configuration, while the dependent variables comprised the three structural measures at the tree level and the three dendrometric parameters at plot-level. The demographic structure of agroforestry species was analyzed in two steps: First, we estimated the diameter growth distributions using the three-parameter Weibull distribution using ForestFit package in R Software (Teimouri 2023). We then analyzed the proportion of trees in four different diameter at breast height (DBH) classes by comparing class frequencies for both agroecological zones. This revealed whether

one zone has a higher abundance of smaller trees (indicating a regeneration focus) or larger trees (suggesting mature trees). Second, a transition probability matrix between classes was calculated using the Kolmogorov–Smirnov probability test for each agroecological zone. These matrices show the probability of trees in a specific diameter class at one time period transitioning to another class in the subsequent period. Comparing these matrices between zones highlights differences in growth dynamics, such as faster or slower transitions between size classes.

Results

Diversity and agroforestry species composition in the two agroecological zones

A total of 1467 agroforestry species across the two agroecological zones (from 221 plots), encompassing 32 species with diverse life forms (including 21 trees and 11 shrubs) from 18 families were identified. The most abundant families were Fabaceae and Bignoniaceae with six and five species respectively. It is noteworthy that 78% of the inventoried agroforestry species were exotic. In the four agricultural landscapes, the most frequent species was *Grevillea robusta* (42.7%), followed by *Mangifera indica* (12.3%) and *Persea anceolat* (11%) (Table 4).

The diversity indices revealed significantly higher values in the Eastern Savannah compared to the Eastern Plateau (Table 5). Specifically, the Shannon and Simpson's indices were calculated as 2.08 and 0.799, respectively, for the East Savannah, whereas for the East plateau, the corresponding values were 1.85 and 0.729. There was a significant difference in the equitability (evenness) of on farm tree species between the two agroecological zones. This suggests that the distribution of woody species in the two zones was not identical.

The Sørensen's similarity coefficient between the eastern plateau and the eastern Savannah was calculated

to be 0.5315, indicating a similarity of approximately 53%. This suggests a moderate level of similarity in woody species composition between the two regions.

Density, Basal area and Crown projected area

Overall, we found an average stem density of 54.6 ± 30.1 trees ha^{-1} . The highest density was recorded in the Eastern Plateau zone (55 trees ha^{-1}), while the Eastern Savannah exhibited a slightly lower density of 47.8 trees ha^{-1} . The analysis of variance (ANOVA) conducted on the stem density (trees ha^{-1}) across different agroecological zones revealed a significant effect (ANOVA, $F(1, 8800) = 209.5$, $p < 0.01$, Tukey HSD, $p < 0.05$). This suggests that there was a statistically significant difference in density ha^{-1} between the agroecological zones. Figure 3 provides a visual representation of the discrepancies between the two agroecological zones in these aspects.

The study revealed significant differences in tree density, basal area, and crown projected area across various strata and agroecological zones. In terms of density per hectare across strata (ANOVA, $F(1, 8800) = 56.49$, $p < 0.01$; Tukey HSD, $p < 0.05$), stratum five displayed the highest density 62.4 trees ha^{-1} , particularly in the Mukama landscape, while the lowest density (27.3 trees ha^{-1}) was observed in the Karama landscape. Basal area and crown projected area also varied significantly across landscapes and zones, with the Eastern Savannah zone showing the highest values. Additionally, the analysis of tree spatial configuration highlighted scattered trees, Boundary, and Mixed dense as the predominant agroforestry systems. Scattered individuals emerged as the dominant configuration, with Boundary showing the highest stem density per hectare. Furthermore, differences in native tree species composition (density per hectare) were evident between landscapes ($W = 210,940$, $p < 0.0001$) (Supplementary Information Fig. 2), with Karama and Nyamugari landscapes exhibiting a higher number of native species. These findings underscore the importance of considering landscape specifics and

Table 5 Richness, Shannon diversity and evenness of different agroecological zones (n = 221)

Agroecology	Species richness	Simpson diversity index	Shannon diversity index	Evenness
East Savannah	26	0.799	2.08	0.3115
East plateau	23	0.729	1.85	0.2840
p-value	< 0.001	< 0.001	< 0.001	< 0.001

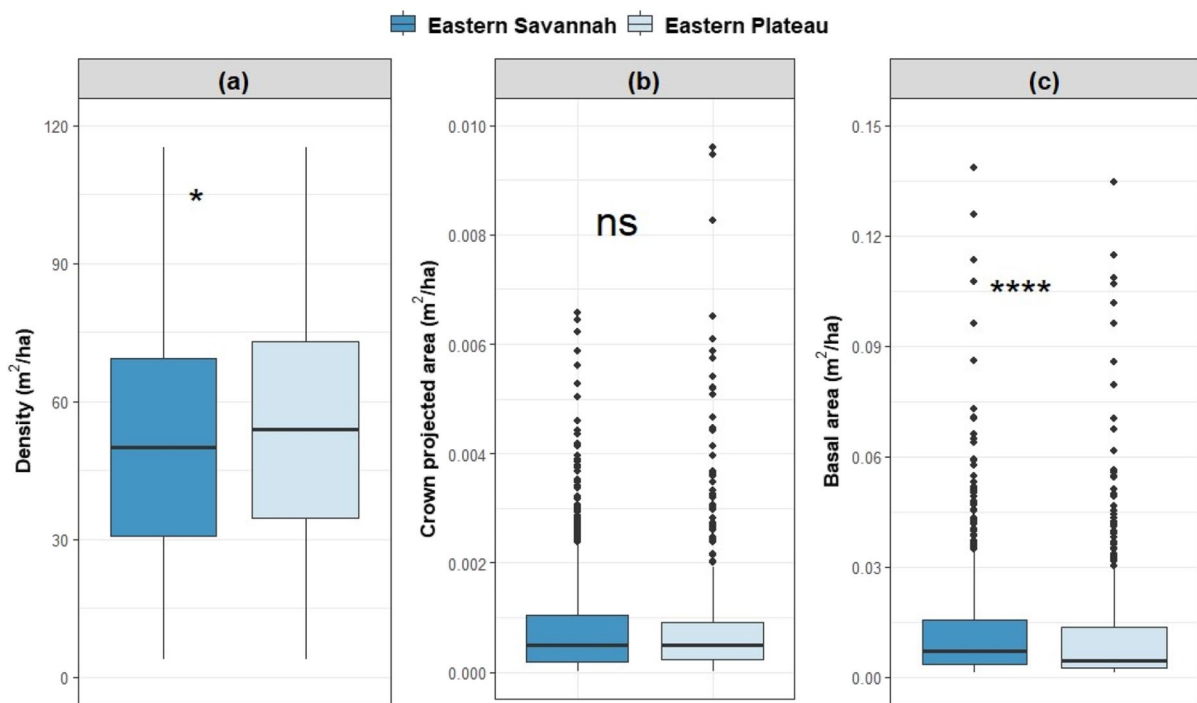


Fig. 3 Changes in plot-level dendrometric parameters within eastern Savannah and eastern plateau. The boxes indicate the 25% and 75% quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles. Sig-

nificant differences in mean in Basal area, crown projected area and stem density as derived from paired t-tests are indicated with asterisks ($p < 0.05$; ns: not significant; **** $p < 0.001$ *** $p < 0.005$ ** $p < 0.01$ * $p < 0.05$)

agroecological in agroforestry management and conservation efforts (Table 6).

Tree structure attributes

The results of the tree structural characteristics indicate the prevalence of smaller agroforestry species across all sampled landscapes. The average tree height in the four landscapes was 6.8 ± 3.4 m with a corresponding average DBH of 10.8 ± 6.9 cm. We found a crown diameter ranging between 0.2 – 5.2 m, with average crown diameter of 2.8 ± 1.8 m across four landscapes.

The largest DBH values were found in stratum six (deep soil > 0.5 m and slope greater than 20 degrees) in the Eastern Savannah. However, species in the Eastern Savannah tended to have broader crowns (average 3.1 m diameter) compared to those in the Eastern Plateau with an average of 2.87 m. Notably, certain *Ficus thonningii* and *Persea americana* exhibited similar crown sizes (4.7 ± 0.76 m and 4.5 ± 0.21 m respectively) across the two agroecological zones (Supplementary Information Table 3).

Importance Value Index

The Importance Value Index (IVI) analysis revealed that *Grevillea robusta* (87.8%), *Mangifera indica* (33.6%), and *Persea americana* (29.7%) were the top three significant species across study region. Specifically, in the East Savannah, the most significant agroforestry species were *Grevillea robusta* (96.8%), *Mangifera indica* (47.9%), and *Persea americana* (25.7%) (Table 7). Conversely, in the East plateau, the three most significant agroforestry species were *Grevillea robusta* (83.9%), *Persea americana* (34.2%), and *Euphorbia tirucalli* (33.7%) (Table 8).

Demographic structure of agroforestry species in the two agroecological zones

As diameter at breast height (DBH) is correlated with tree growth rate and age (Numbisi et al. 2021), we categorized agroforestry species into four different diameter classes to depict various growth forms: 1 = Very small: (4 – 10 cm] DBH; 2 = Small: DBH

Table 6 Summary of the dendrometric parameters (i.e., densities, basal area and crown projected area) of the species encountered across different spatial configuration in the four landscapes study area ~250,000 ha; considering hillside agriculture land, with a total of 1467 detected trees. Tree density and basal area per ha were calculated only for trees with > 4 cm

DBH. Here we focused on three types of spatial configurations that were the most predominant in the agricultural landscapes of the study region (Mixed sparse (i.e., scattered wooded trees in the farmland), Boundary (i.e., trees on edges of plots/fields) and Mixed dense (i.e. trees in block)

Dendrometric parameters	Spatial configuration	Eastern Plateau		Eastern Savannah		p-Value
		Gikomero	Karama	Mukama	Nyamugari	
Density (trees ha ⁻¹)	Mixed sparse	55.8	25	61.9	46.6	0.0001
	Mixed dense	56.1	41.1	45.4	49.7	0.0025
	Boundary	66.2	29.2	67.2	22.1	0.0001
Basal area (m ² ha ⁻¹)	Mixed sparse	0.63	0.8	0.7	0.55	0.2463
	Mixed dense	0.63	0.4	0.56	0.8	0.0003
	Boundary	0.69	0.64	0.48	0.34	0.0003
Crown projected area (m ² ha ⁻¹)	Mixed sparse	35.7	53.1	39.9	34	0.0001
	Mixed dense	38.4	24.2	25.5	23.6	0.0001
	Boundary	31.9	35.5	38	45	0.0008
Species richness	Mixed sparse	12	8	10	11	0.0209
	Mixed dense	8	6	6	9	0.0202
	Boundary	9	4	6	3	0.079

(10 – 20 cm]; 3 = Large: DBH (20 – 30 cm]; 4 = Very large: DBH (30 – 60 cm]. The results of the diameter distribution using a three-parameter Weibull distribution show a strong fit for the diameter distribution in both Eastern Savannah and Eastern Plateau agroecological zones. The distribution of tree individuals across size classes exhibited a right-skewed pattern, indicating a trend where trees tend to vanish before attaining larger sizes (Supplementary Information Fig. 4).

The vast majority of transitions were one stage upward: Very small (DBH 4–10 cm): 0.559 (5.98%)—indicating that only a small proportion of trees in this size class remained within it. Very small—Small (DBH 10–20 cm): 0.201 (20.12%)—a significantly higher proportion of trees transitioned from the very small class to the small class. Small—Large (DBH 20–30 cm): 0.278 (27.83%)—suggesting a moderate transition rate from the small to large size class. Large—Very large (DBH 30–60 cm): 0.031 (3.13%)—with the transition rate from large to very large appearing to be the lowest. The average tree diameter at breast height (DBH) in this study region 10.8 cm. Notably, the size class of 10–20 cm (Small) held particular importance. The transition probability from this class (0.2) implies that only 20% of trees can grow into the next size class. This finding

suggests a potential limitation of resources necessary for significant tree growth within this specific region.

Discussion

Assessing the diversity and composition of agroforestry systems across various agroecological zones is crucial for guiding the selection of species suited to macroclimatic conditions and farming systems. Our study offers a quantitative characterization of tree occurrence and contrasts among the agroecological zones, namely the Eastern Savannah and Eastern Plateau of Rwanda. To our knowledge, this is the first study to comprehensively characterize agroforestry species, encompassing tree diversity, species composition, and demographic structure perspectives of agroforestry species in the study region.

Diversity and agroforestry species composition in Eastern Savannah and east plateau

Diversity indices revealed a significant difference in agroforestry species between the Eastern Savannah and Eastern Plateau. The Eastern Savannah exhibited higher diversity values compared to the Eastern Plateau. This aligns with the finding that the Eastern

Table 7 Agroforestry Species Relative Density (RD %), Relative Frequency (RF %), Relative Dominance (RDo%) and Importance Value Index (IVI) in Eastern Plateau

N ⁰	Scientific Name	Local Name	RF(%)	RDo (%)	RD(%)	IVI (%)
1	<i>Grevillea robusta</i> A.Cunn. ex R.Br.A.Cunn. ex R.Br.A.Cunn. ex R.Br.	Gereveriya	38.2	36.1	9.6	83.9
2	<i>Persea americana</i> Mill	Avoka	12.2	17.7	4.3	34.2
3	<i>Euphorbia tirucalii</i> L	Umuyenzi	14.1	11.3	8.3	33.7
4	<i>Mangifera indica</i> L	Umwembe	11.0	7.9	5.6	24.5
5	<i>Markhamia lutea</i> (Benth.) K.Schum	Umusave	7.4	3.8	6.1	17.4
6	<i>Toona sinensis</i> (A.Juss.) M.Roem	Isederi	1.8	2.3	7.2	11.3
7	<i>Jacaranda mimosifolia</i> D.Don	Jakaranda	1.3	1.0	7.8	10.0
8	<i>Ficus thonningii</i> Blume	Umuwumu	1.4	5.7	2.8	9.9
9	<i>Eucalyptus saligna</i> Sm	Inturusu	2.5	2.2	4.4	9.2
10	<i>Combretum pisoniiflorum</i> (Klotzsch) Engl	Umurama	0.6	0.6	7.8	9.0
11	<i>Carica papaya</i> L	Ipapayi	2.4	2.3	2.7	7.3
12	<i>Kigelia africana</i> (Lam.) Benth	Umuwungavungo	0.3	2.5	3.1	5.8
13	<i>Ricinus communis</i> L	Ikibonobono	2.1	0.6	2.9	5.6
14	<i>Citrus × limon</i> (L.) Osbeck	Indimu	0.6	0.5	3.9	5.0
15	<i>Ziziphus abyssinica</i> Hochst. ex A.Rich	Umukugutu	0.1	2.6	1.6	4.3
16	<i>Macademia ternifolia</i> F.Muell	Makadamiya	0.5	0.4	3.1	4.0
17	<i>Senna spectabilis</i> (DC.) H.S.Irwin and Barneby	Kasiya	1.3	0.5	2.2	4.0
18	<i>Leucaena leucocephala</i> (Lam.) de Wit	Lesena	0.5	0.1	3.1	3.7
19	<i>Gymnanthemum amygdalinum</i> (Delile) Sch.Bip	Umubirizi	0.6	0.3	2.6	3.5
20	<i>Markhamia obtusifolia</i> (Baker) Sprague	Umukundambazo	0.1	0.6	1.6	2.3
21	<i>Osyris lanceolata</i> Hochst. and Steud	Kabaruka	0.1	0.4	1.6	2.0
22	<i>Solanecio mannii</i> (Hook.f.) C.Jeffrey	Umutagara	0.3	0.1	1.6	1.9
23	<i>Erythrina abyssinica</i> Lam	Umuko	0.1	0.2	1.6	1.9
24	<i>Psidium guajava</i> L	Ipera	0.1	0.1	1.6	1.8
25	<i>Zanthoxylum chalybeum</i> Engl	Intare y'irungu	0.1	0.1	1.6	1.8
26	<i>Spathodea campanulate</i> P.Beauv	Umunyara	0.1	0.0	1.6	1.7

Savannah harbored the highest number of native tree species. Additionally, the planting of exotic tree species on the Eastern Plateau likely contributed to the lower diversity observed in that region. The Eastern Plateau displayed a lower Shannon Diversity Index (1.85) compared to the Eastern Savannah (2.08). In ecological studies, a Shannon Diversity Index value of 2 is considered the threshold for medium diversity (Barbour et al. 1980). Therefore, this study suggests that the Eastern Plateau's agricultural landscapes are dominated by a smaller number of woody plant species compared to the Eastern Savannah.

In all landscapes, exotic tree species represent approximately 78% of the total number of trees recorded, with the eastern Savannah accounting for up to 49.78%. The four most common and dominant

tree species planted were *Grevillea robusta*, a tree species used mainly for timber and preferred for their fast growth that can enable farmers to get various benefits within a short period of time (Pedercini and Dawson 2022) followed by *Mangifera indica* and *Persea americana* mainly used for fruit production for food and *Euphorbia turcalii* mainly used as hedgerow and farm plot delineation (Ndayambaje 2013). In the study area, tree resources are scarce (Bucagu et al. 2013; Iiyama et al. 2018; Ndayambaje et al. 2014), and the prevalence of *Grevillea robusta* may be due to its fast growth and production of timber, firewood as well as sticks for climbing beans (Bucagu 2013; Cyamweshi et al. 2023). The occurrence of a large number of exotic tree species in the landscape study sites could be explained by the fact that in the Eastern

Table 8 Agroforestry Species Relative Density (RD %), Relative Frequency (RF %), Relative Dominance (RDo%) and Importance Value Index (IVI) in Eastern Savannah

N ⁰	Scientific Name	Local Name	RF(%)	RDo (%)	RD(%)	IVI (%)
1	<i>Grevillea robusta</i> A.Cunn. ex R.Br.A.Cunn. ex R.Br.A.Cunn. ex R.Br	Gereveriya	48.1	34.7	14.0	96.8
2	<i>Mangifera indica</i> L	Umwembe	13.9	26.0	8.0	47.9
3	<i>Persea americana</i> Mill	Avocado	5.2	16.1	4.3	25.7
4	<i>Carica papaya</i> L	Ipapayi	8.8	6.1	10.0	24.9
5	<i>Eucalyptus saligna</i> Sm	Inturusu	5.8	2.5	7.3	15.5
6	<i>Euphorbia tirucalii</i> L	Umuyenzi	7.4	2.3	4.9	14.6
7	<i>Markhamia lutea</i> (Benth.) K.Schum	Umusave	3.1	2.3	6.5	11.9
8	<i>Ficus thonningii</i> Blume	Umuwumu	0.7	4.6	2.3	7.7
9	<i>Ziziphus abyssinica</i> Hochst. ex A.Rich	Umukugutu	0.4	0.3	5.6	6.4
10	<i>Gymnanthemum amygdalinum</i> (Delile) Sch.Bip	Umubirizi	1.0	0.2	4.3	5.6
11	<i>Toona sinensis</i> (A.Juss.) M.Roem	Isederi	0.9	0.8	3.7	5.4
12	<i>Dombeya torrida subsp. torrida</i>	umukore	0.6	0.7	3.7	5.0
13	<i>Senna spectabilis</i> (DC.) H.S.Irwin and Barneby	Kasiya	1.2	0.2	3.0	4.4
14	<i>Citrus × limon</i> (L.) Osbeck	Indimu	0.6	0.1	3.7	4.4
15	<i>Vachellia hockii</i> (De Wild.) Seigler and Ebinger	Umugenge	0.3	0.3	3.7	4.3
16	<i>Albizia petersiana</i> (Bolle) Oliv	Umumeyu	0.3	1.2	1.9	3.4
17	<i>Olea europaea subsp. cuspidata</i> (Wall. and G.Don) Cif	Umunzenze	0.1	1.0	1.9	3.0
18	<i>Solanecio mannii</i> (Hook.f.) C.Jeffrey	Umutagara	0.4	0.1	1.9	2.5
19	<i>Ricinus communis</i> L	Ikibonobono	0.3	0.1	1.9	2.3
20	<i>Vepris nobilis</i> (Delile) Mziray	Umuzo	0.3	0.1	1.9	2.2
21	<i>Combretum pisoniiflorum</i> (Klotzsch) Engl	Umurama	0.1	0.0	1.9	2.0
22	<i>Senna didymobotrya</i> (Fresen.) H.S.Irwin and Barneby	Umucyuro	0.1	0.0	1.9	2.0
23	<i>Leucaena leucocephala</i> (Lam.) de Wit	Lesena	0.1	0.0	1.9	2.0

province of Rwanda, which is considered a semi-arid region of Rwanda, native trees were cut down for agricultural intensification following the conversion of pastureland, particularly in Umutara, into cropland over the past decades (MINAGRI 1988).

Moreover, the high number of exotic agroforestry species in the two agroecological zones likely stems from extensive tree planting focused on fast-growing species to mitigate drought and its associated negative impacts. This approach might positively influence local rainfall patterns (Shema and Lanhai 2024). The retention of native trees in the two agroecological zones highlights the importance of native species in supporting landscape ecosystem services, such as cultural services. However, due to a lack of research and limited availability of native species, they are not promoted in these landscapes. Consequently, the misconception persists that farmers simply do not prefer them. Agroforestry with native species could

also serve as habitat for native biodiversity, thereby helping to conserve and counteract the loss of species from natural forests (Barrios et al. 2018). Hence, we suggested that promoting native tree species in agricultural landscapes can boost landscape sustainability and hence increase production (Gemechu et al. 2021). Moreover, native trees attract native birds, insect pollinators, and other arthropods biodiversity which could benefit adjacent agriculture (Barrios et al. 2012; Nsengimana et al. 2021; Valdés et al. 2020).

The retention and planting of on farm trees depend heavily on both a strong sense of ownership by farmers and stewardship practices (Bucagu et al. 2013; Cyamweshi et al. 2023). However, this study shows that landscape structure and land-use intensity also play a crucial role, as evidenced by previous studies (Fikir et al. 2018; Ndayambaje et al. 2012). Similar research in the region suggests that farmer perceptions, such as tree-crop interplay, significantly

influence tree removal or retention decisions (Ndayambaje et al. 2012). Our study supports this, with findings that native trees like *Zanthoxylum chalybeum* are primarily retained for medicinal use by traditional healers. Conversely, exotic species like *Grevillea robusta* cultivated in agricultural landscapes for its multipurpose use i.e., timber production, firewood, stakes for climbing beans among others. Additionally, some exotic trees like *Persia americana* (avocado) and *Mangifera indica* (mango) provide fruits for household consumption and income generation (Ndayambaje 2013). Large native solitary trees like *Albizia petersiana* might also be retained for cultural purposes (supporting beehives) and environmental benefits (shelter and soil improvement). Interestingly, Karama landscape exhibits a high number of native species, similar to Nyamugari landscape. This could be because native species in these areas are better adapted to the local climate and challenges like pests and diseases (Ndayambaje et al. 2014), highlighting how landscape variations can influence farmer decisions and the resulting tree species composition.

Density, basal area, and crown projected area

Tree density in tropical agricultural landscapes varies significantly, influenced by methodological approaches, size thresholds, sampled trees, local conditions, and management practices (Korol et al., 2021). Our study observed an average tree density of 54.6 trees ha⁻¹ (terrestrial sampling), which is slightly lower than the 79.6 trees ha⁻¹ reported by Mugabowindekwe et al. (2022) using remote sensing for Rwandan farmlands. This discrepancy likely stems from their inclusion of smaller trees (diameter at breast height, DBH, < 4 cm) compared to our minimum DBH of 4 cm. Additionally, remote sensing in these agroecological zones might confuse trees with banana plantations, a common feature (Table 1), leading to overestimations. Therefore, we argue for the limitations of relying solely on satellite imagery for tree density determination.

We found that tree density per hectare varied a lot across landscapes. This suggests the influence of landscape-specific farming systems and climate conditions. For instance, despite the presence of steep terrain (Fig. 1), our findings reveal a high number of on-farm trees in both Mukama and Gikomero landscapes with 67.2 trees ha⁻¹ and 66.2 trees

ha⁻¹ respectively. However, 46.9 trees in Nyamugari and Karama, and 35.9 trees in both, falling below the overall average (54.6 trees ha⁻¹).

Variations in tree densities also differed within and across strata. While our study did not focus on specific landscape structure variables influencing woody species distribution, we found that slope, along with soil depth, explains the variability patterns within the studied agroecological farming systems. Among the four landscapes, stratum five displayed the highest stem density (62.4 trees ha⁻¹), while the lowest was observed in the Karama landscape's stratum two (27.3 trees ha⁻¹). The observed low tree densities in Karama (east plateau) and Nyamugari (east Savannah) are unexpected given their high percentage of potentially suitable areas for agroforestry (Supplemental Information Table 2). Similar to Ndayambaje et al. (2014), limited access to climate-resilient tree resources, inadequate species-site matching, historical deforestation, and prevailing land-use patterns might explain the low agroforestry cover in both Karama and Mukama landscapes.

The highest basal areas were observed in the Eastern Savannah, notably in the Nyamugari landscape (0.67 m² ha⁻¹). This coincides with our finding that Nyamugari landscapes exhibit a high number of native species. This suggests that the retained native species in agricultural landscapes tend to have larger DBH and can contribute more significantly to the overall stem volume and potential above ground biomass (AGB) compared to exotic species.

In this study, crown projected area, estimated from crown diameter, did not differ significantly between the Eastern Plateau and Eastern Savannah agroecological zones. This suggests that crown projected area may not be the most effective indicator for comparing the AGB in agricultural landscapes. Our findings align with those of (Somarriba et al. 2024), who praise the value of modern tools such as smartphone applications, drone-based high-resolution photography, and LIDAR for canopy cover assessment (Blaser et al. 2018; Mugabowindekwe et al. 2024). However, tree density and basal area remain valuable surrogate variables for aboveground biomass estimation. Recording and reporting these metrics is crucial to understand the interaction between agroforestry trees and crops, soil nutrients and water balance and in agroforestry systems. Therefore, including information on the tree stem diameter distribution would

further enhance the utility of density and basal area data for describing tree stock yields in agricultural landscapes.

Overall, the results confirm that the four agricultural landscape were different, suggesting the effect of agroecological systems, with low density of native tree species likely related to the conversion of pasture land to agricultural land in the last two decades (MINAGRI 1988). Agroforestry species in the studied landscapes may still be at an early stage of agroforestry establishment due to the fairly recent tree planting movement across the country (MoE 2019). Contrary to our initial hypothesis, areas with extensive forest cover tend to have a higher densities of on-farm trees. This can be explained in two ways. First, farmers in such regions may allocate less suitable land for tree plantations rather than attempting difficult cultivation (Fig. 1). Second, the readily available fuelwood from the surrounding forests (Table 2) frees farmers to dedicate their on-farm trees for other critical purposes, like soil conservation and erosion control.

Structural characteristics of agroforestry species

Our findings on derived relationship between tree structural attributes, indicate that agroforestry species-specific structural attributes can play a crucial role in determining the spatial configuration of trees on farms. For example, factors like crown size (e.g., crown projected area) and its predicted growth expansion, coupled with ecological requirements of individual tree species, influence farmers' decisions on where and how to plant agroforestry trees—whether in lines, scattered, or in blocks (Pretzsch et al. 2015). In our study, we found that trees planted in blocks exhibited the largest crown size, with an average of 4.7 ± 0.76 , followed by those planted in scattered patterns and in lines, respectively. Fruit trees such as *Mangifera indica* and *Persea americana* were predominantly found in block plantings, while *Grevillea robusta* was the dominant species in line plantings, possibly indicating farmers' anticipation of heavy pruning as the trees develop.

The two agroecological zones revealed variations in tree structural attributes, both within strata and between landscapes. This variation within and between landscapes highlights the influence of agroecological systems on tree structure. The Eastern

Savannah exhibited a slightly larger average DBH compared to those in the East Plateau, indicating potential differences in growth rates and maturity levels. *Ficus thonningii* displayed consistent DBH values across both zones (22.9 ± 4.21), suggesting robust growth characteristics regardless of environmental conditions, we found no significant difference in average crown size between the two agroecological zones when viewed all together (Fig. 4). This may reflect similar sunlight and shade effects across the two agroecological zones. Height measurements, however, revealed significant differences between the zones. Species in the Eastern Savannah were generally taller (average 10.55 m) compared to those in the Eastern Plateau (average 9.85 m). This suggests different environmental influences on vertical growth patterns in both zones. Interestingly, *Eucalyptus saligna* maintained consistent height within and across zones, highlighting its inherent growth characteristics that are independent of agroecological variations.

Tree height was found to be closely correlated with the diameter at breast height (DBH), exhibiting a linear relationship with a correlation coefficient exceeding 50% for only two species, namely *Eucalyptus saligna* ($R^2=0.75$; $y=1.4+0.9x$) and *Grevillea robusta* ($R^2=0.60$; $y=3.3+0.45x$), highlighting the importance of considering such factors for accurate inventory and management practices. Conversely, for other species, the correlation between tree height and DBH was comparatively weaker (supplementary information Fig. SI 3).

Furthermore, the relationships between tree species-specific crown diameter and stem diameter suggest that predictions were not significant for *Eucalyptus saligna* ($R^2=0.39$; $y=2.1+0.09x$) and *Grevillea robusta* ($R^2=0.16$; $y=2.1+0.09x$), indicating that pruning effects, which are species-specific, heavily influence these regression relationships. Moreover, the relationship between DBH and crown diameter showed a robust correlation in *Ficus thonningii* ($R^2=0.73$). This highlights the challenge of accurately predicting diameter at breast height (DBH) from crown diameter in agroforestry landscapes, emphasizing the need for ground-based measurements as ground truthing for better prediction of aboveground wood biomass and carbon stocks for instance.

Overall, although the ecosystem services perceptions by farmers may determine the adoption rate of trees on farms (Bucagu et al. 2013; Derero et al. 2021),

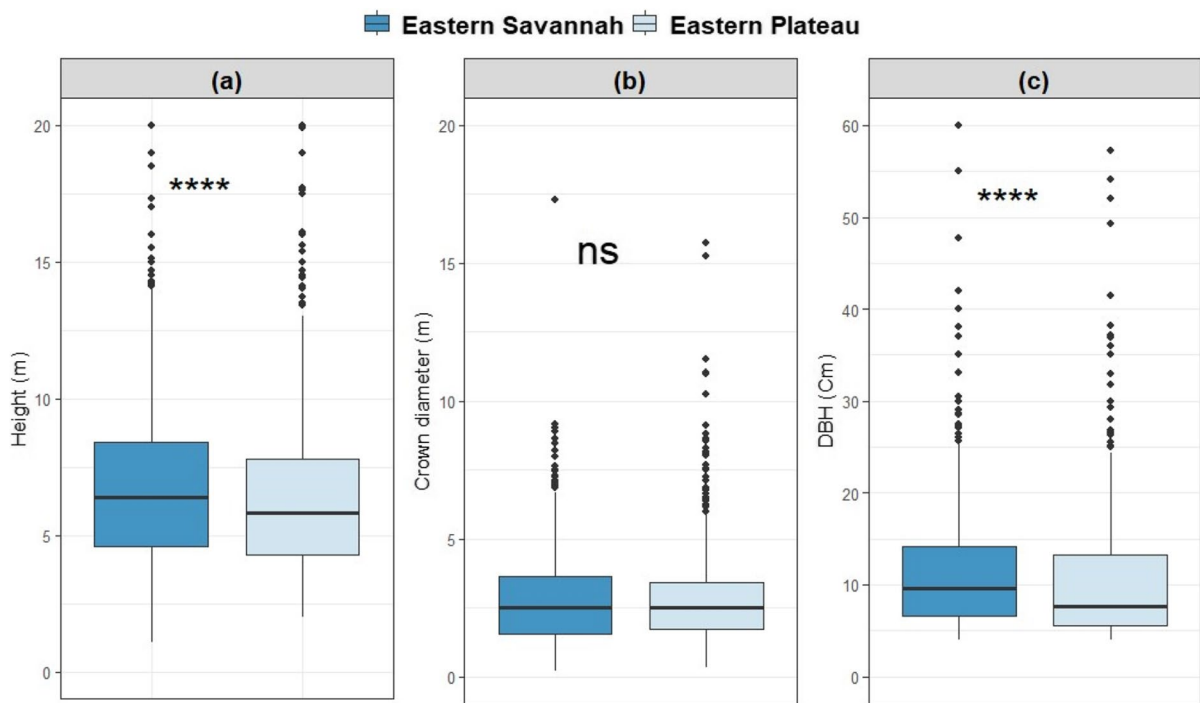


Fig. 4 Comparison of tree structural attributes within eastern Savannah and eastern plateau. The boxes indicate the 25% and 75% quartile, with a median line and 2 whiskers showing the 10% and 90% quantiles. Significant differences in mean diam-

eter at breast height, crown diameter and height as derived from paired t-tests are indicated with asterisks ($p < 0.05$ ns: not significant; 0****0.001***0.005**0.01*0.05)

here, we argue that the anticipated individual structural properties indicate that choice of agroforestry species to be planted or retained might depend on its structural attributes apart from socio ecological factors.

Important Value index

In agroecology, tree species with a high Importance Value Index (IVI) are considered more significant than those with a low IVI. There are several reasons for the significant value attributed to maintaining tree species on farmland. These include their broader economic roles (Murthy et al. 2017) and their ecological adaptation to environmental conditions (Approach 2008; Eyasu et al. 2020) IVI serves as a crucial parameter for prioritizing species for conservation (Murdjoko et al. 2016). Species with high IVI values require less conservation priority, whereas those with low IVI values demand greater conservation efforts.

In our study, we argue that native trees such as *Zanthoxylum chalybeum*, *Olea europaea*, and *Osyris lanceolata* were predominantly retained in the study

area due to their traditional medicinal uses by local healers. Conversely, some exotic trees are being cultivated on farms primarily for timber production, such as *Grevillea robusta*, *Toona sinensis*, and various species of *Eucalyptus*. Additionally, other exotic tree species are planted for their production and provisioning services, including household consumption of fruits (e.g., *Persia americana*, *Mangifera indica*, *Psidium guajava*, *Citrus × limon*, *Macadamia ternifolia*), as well as for generating income. Moreover, large solitary native trees like *Albizia petersiana* and *Erythrina abyssinica* may have been retained for their cultural and supportive services, such as hosting traditional beehives, providing shelter, and improving soil fertility. Therefore, given the lower value of native species, we recommend that tree planting initiatives focus on planting native species due to the widespread adoption of exotic species. However, priority should be given to conserving the remaining large solitary trees for their cultural and ecological significance including biodiversity conservation in agricultural landscapes.

Demographic structure of agroforestry species

Comparing the demographic structures of agroforestry species between the two agroecological zones revealed striking similarities. The transition probability of the trees transitioning from one diameter class to another, offering valuable insights into the agroforestry species growth dynamics and potential alterations in diameter composition over time. In both zones, the DBH class distribution with the highest proportion of species consisted of class with small trees with over 80% of agroforestry species found in the first lower DBH class. This underscores the prevailing size structure of agroforestry species within each zone, predominantly characterized by young trees.

Land use and tree legacy in agriculture landscapes

Our study indicates a concerning prevalence of exotic tree cover at the landscape scale within agricultural environments. This prevalence carries potential negative implications for biodiversity conservation within these landscapes. While landscape-level planning is crucial, it may not sufficiently address the requirements of individual trees and their role in biodiversity maintenance. Focusing on the ecological perspective and management of individual trees within the landscape could potentially enhance functional agrobiodiversity (Van Den Berge 2021; Pa et al. 2024; Paul 2018). Numerous studies demonstrate the significance of large solitary trees in biodiversity conservation (Bolívar-Santamaría and Reu 2021; Jones et al. 2018; Silva et al. 2020; Zotarelli et al. 2019). These trees can act as stepping stones for birds, aiding in predator detection and movement (Silva et al. 2020).

Historical land-use changes such as deforestation or conversion to agriculture can fragment existing landscapes, disrupting crucial connections and diminishing overall habitat stability, thereby impacting biodiversity (Pa et al. 2024; Tscharnkte et al. 2011). For instance, past land use can facilitate the introduction or proliferation of certain species, often invasive ones, while displacing native flora and fauna (Pa et al. 2024). This alteration in species composition disrupts ecological equilibrium and diminishes biodiversity. However, there is a lack of evidence regarding the landscape-scale impact of agroforestry on functional biodiversity in the studied landscapes (SANBI 2022).

Understanding the landscape structure and land use legacy is crucial for devising effective conservation

strategies in Rwanda, particularly in the studied agroecological zones. A recent spatial biodiversity assessment in Rwanda identified techniques such as restoring native vegetation, managing invasive species, and establishing corridors between fragmented habitats to alleviate negative impacts and promote biodiversity recovery (SANBI 2022). Nonetheless, the effects of land-use legacy can persist for decades or even centuries. Soil recovery can be sluggish, and fragmented habitats may take a considerable time to naturally reconnect. Therefore, targeted interventions should prioritize the protection and promotion of the growth and well-being of existing large solitary trees in agricultural landscapes (Barrios et al. 2018). We contend that this approach has the potential to enhance biodiversity conservation, the ecosystem services provided by trees, and overall resilience within agricultural landscapes (Barrios et al. 2018; Sritongchuay et al. 2022).

Conclusions

This study examined the diversity and composition of agroforestry species in Rwanda's Eastern Plateau and Eastern Savannah zones. A concerning trend emerged: the number of trees drastically declines with increasing size. This skewed diameter distribution suggests unsustainable harvesting, with trees cut before maturity. This highlights the pressure local communities place on their vital tree resources. Surprisingly, higher forest cover coincided with more on-farm trees. This challenges the initial hypothesis – perhaps these areas have less arable land due to steep slopes or poor soil, leading to increased tree cover. Additionally, readily available fuelwood from surrounding forests allows farmers to use on-farm trees for other purposes like soil conservation. Variations in tree composition were observed, with the versatile *Grevillea robusta* dominating. Notably, most trees were small and scattered, with limited potential for timber due to early harvesting. This study provides valuable data for conservation efforts. It identifies priority species and underscores the importance of incorporating native trees into restoration initiatives alongside the currently prevalent exotic species. Further research is recommended to explore the ecological impact of these exotic tree-dominated landscapes and include additional habitat types for a more comprehensive understanding of the region's historical land use, tree legacy, and overall ecosystem function.

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Data availability The raw data supporting the discussion and conclusion of this article will be made available by the authors, upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interests The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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