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Leaf functional traits and farmer knowledge predict decomposition of shade-tree leaves in Colombian cacao agroforestry

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Abstract Poor soil fertility is a major cause of low productivity in smallholder cacao (*Theobroma cacao* L.) plantations. In cacao agroforestry, both cacao trees and associated shade trees can influence soil fertility via the decomposition of leaf litter or pruning residues. These organic inputs can increase soil organic matter content and nutrient availability, yet their contribution varies widely among tree species. This highlights the importance of selecting appropriate shade tree species, which can be informed by farmers' knowledge. We measured leaf decomposition rates of shade trees commonly used in cacao agroforestry in Colombia to examine whether species functional traits can predict these rates and evaluated how these findings align with farmers' perceptions. A common garden experiment was established to assess leaf decomposition of 15 shade tree species and cacao, with leaves collected from 46 cacao agroforestry systems across the country. For each species, we measured or compiled data on 12 functional traits, including leaf nitrogen-, phosphorus-, potassium-, carbon-, calcium-, and chlorophyll content, specific leaf area, and carbon-to-nitrogen ratio, along with maximum height, wood density, deciduousness, and nitrogen-fixing ability. Farmers were asked to free-list shade tree species based on their perceived leaf decomposition rate and contribution to soil fertility. Our results show that leaf nutrient contents predict leaf decomposition rates and that farmers' knowledge closely reflects these experimental results. This study emphasizes the role of fast-growing, resource-acquisitive species in enhancing nutrient cycling and highlights the value of farmers' ecological knowledge in guiding shade tree selection in cacao agroforestry.

Keywords Common garden experiment · Leaf decay · Local ecological knowledge · Nutrient cycling · Soil fertility · *Theobroma cacao* · Tree species selection

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Introduction

Smallholder cacao (*Theobroma cacao* L.) production systems are generally characterized by low yields, undermining farmer livelihoods and environmental sustainability goals, particularly considering the rising global demand for cocoa products (Abbott et al. 2018; Kongor et al. 2019). Poor soil fertility, defined as the soil's ability to support plant growth (Stockdale 2002), is among the main causes of low cacao productivity. It results from repeated nutrient removal through cacao harvest, low or non-existent application of fertilizers (Bai et al. 2022) and nutrient losses through soil erosion (Amponsah-Doku et al. 2022). This is particularly the case in cacao monocultures, which have been found to frequently face negative nutrient balances, especially for potassium (Hartemink 2005; Hougni 2023).

Cacao agroforestry systems (AFS), which combine cacao cultivation with shade tree species, can mitigate low soil fertility by improving overall soil health (Pérez-Flores et al. 2018; Visscher et al. 2024), i.e. the capacity of soil to perform its multiple ecological functions within ecosystem and land-use boundaries (Bünemann et al. 2018), including supporting plant growth. Shade trees can moderate microclimatic conditions (Tscharntke et al. 2011; Rodriguez et al. 2021) and cover the soil with diverse leaf litter, helping conserve soil moisture and enhancing soil organic matter (Cotrufo et al. 2015; Schneidewind et al. 2019; Khulpu et al. 2025). In addition, the deeper and more diverse root systems of shade trees may improve the soil's structure and nutrient and water holding capacity, and contribute to erosion control (Bargués Tobella et al. 2014; Sauvadet et al. 2020; de Carvalho et al. 2021; Suárez et al. 2021; Rodriguez et al. 2021). However, evidence is mixed, as not all studies have found consistent positive effects of cacao AFS on soil fertility (Blaser et al. 2017; Niether et al. 2020). More research is needed to better understand which tree characteristics, if any, drive the potential enhancement of soil health and associated soil fertility.

The potential nutrient benefits of shade trees for cacao plants arise from different underlying mechanisms. Shade trees can capture additional nutrients not accessible to cacao trees, either by fixing atmospheric nitrogen (e.g. in the case of leguminous trees), or by mobilizing nutrients from soil layers below cacao's relatively shallow rooting zone (Mortimer et al. 2018). Further, shade trees reduce erosion and associated nutrient losses. A diversity of shade trees (rather than a single species) may further increase nutrient partitioning. Over time, nutrients absorbed by shade trees are returned to the soil through the deposition of litter and pruned biomass, resulting in the release of nutrients as organic matter decomposes (Lohbeck et al. 2015; Pérez-Flores et al. 2018; Cerda et al. 2019). However, the extent to which decomposition contributes to nutrient input is influenced by species identity and associated functional traits (Kattge et al. 2020; Bai et al. 2022), calling for careful selection of tree species for improving soil fertility in AFS (Sauvadet et al. 2019). The role of different shade tree species on nutrient dynamics in cacao is a major knowledge gap limiting optimal cacao AFS design (Niether et al. 2020; Visscher et al. 2024).

Plant functional traits provide a useful framework to guide species selection in AFS (Finegan et al. 2015; Martin and Isaac 2015; Tubenchlak et al. 2021). Both 'hard' traits (i.e. traits directly related to ecosystem functions but relatively difficult to measure, e.g. nitrogen fixation rate) and 'soft' traits (i.e. easier-to-measure traits that can be used as proxies, e.g., specific leaf area) can be used to support tree species selection (Thomas et al. 2017; Fremout et al. 2022). Shade tree species with leaf functional traits most dissimilar to cacao have been shown to be most effective in improving soil functions such as plant available phosphorus, soil nitrate content and overall biochemical fertility (Sauvadet et al. 2020). Leaf traits, in particular, have been identified as the primary drivers of leaf litter decomposition rates (Cassart et al. 2020), outweighing the influence of climatic conditions and soil quality (Cornwell et al. 2008; Castillo-Figueroa et al. 2025). Among these, leaf nitrogen concentration, specific leaf area (SLA) and chlorophyll content have been found to predict decomposition dynamics (Santiago 2007; Bakker et al. 2011; Bai et al. 2022; Castillo-Figueroa et al. 2025). These relationships align with the leaf economics spectrum (LES), a global spectrum of leaf trait variation ranging from resource-acquisitive species with soft, nutrient-rich short-lived leaves to resource-conservative species with tough, nutrient-poor, long-lived leaves (Reich 2014; Díaz et al. 2016; Onoda et al. 2017), the latter of which are lower

decomposition rates. While the relation between the LES and leaf decomposition is largely understood (Reich 2014), it has rarely been applied as a practical tool to guide tree species selection in cacao agroforestry (Suárez et al. 2021).

Agroforestry used to be the dominant approach to agriculture in much of the humid tropics prior to the global homogenization towards high-input low-diversity farming systems (Raj and Lal 2014). Much traditional ecological knowledge regarding agroforestry practices remains or has been (re)acquired through empirical observation. This knowledge, more accurately termed local ecological knowledge (LEK) (Berkes et al. 2000), provides unique and complementary insights to scientific approaches (Thomas 2009; Thomas et al. 2017; Fremout et al. 2021). Farmers in Central America and West Africa have been shown to select shade trees in agroforestry systems through an implicit understanding of their leaf functional traits (Martin and Isaac 2015). Integrating Western and local knowledge systems is therefore key to improve agroforestry system design and their adaptation to diverse local contexts (Schwinning et al. 2022).

Beyond species selection, also the design (e.g. shade tree density) and management of agroforestry systems play a role in the soil fertility effects of these systems. Pruning of shade trees, in particular, increases light availability to cacao and increases nutrient input by decomposition of pruned residues which has the potential to boost flowering and pod production, respectively, and thereby increase cacao yields (Esche et al. 2023; Saj et al. 2025). Active pruning increases not only the quantity but also the quality of organic inputs to the soil: freshly pruned leaves contain higher concentrations of essential plant nutrients than senescent leaves and tend to decompose more rapidly (Guo et al. 2024). As such, studying the decomposition of pruned leaves can directly inform recommendations on both shade tree selection and management.

The present study aims to advance understanding of the interplay between shade tree functional traits and leaf decomposition as a proxy for nutrient cycling in cacao agroforestry systems. Specifically, we investigate how functional traits of commonly used shade tree species influence decomposition rates measured in a common garden experiment, and to what extent these rates align with farmers' LEK. We hypothesize that shade tree functional traits related to an acquisitive resource use strategy (e.g. high nutrient contents) are associated with higher leaf decomposition rates and that these findings and the corresponding LEK are congruent.

Materials and methods

Study region

We visited 46 smallholder farms (productive size 1–15 ha) with cacao agroforestry systems (with ages 5–60 years) distributed across the Colombian departments of Tolima (15 farms), Boyacá (13), Cesar (9) and Santander (9) (Figure S1). These departments, and the farms visited, were selected to represent a variety of cacao growing areas while also considering logistic feasibility. Elevation in the sampled farms ranged from 736 to 1106 masl, average annual temperature ranged from 22.0 to 24.3 °C, while annual precipitation varied between 1724 and 2310 mm. The most common soil types at these locations include cambisols, ferralsols and acrisols. A summary of the environmental conditions at the sampled farms is provided in Table S2.

Local ecological knowledge

At each farm we asked the farmer present ($n = 46$, among which 5 women) to (1) free-list the tree species present on their farm that decompose most rapidly and those that decompose mostly slowly, and (2) to free-list the species they perceive as improving or reducing soil fertility. Free-listing is a method in which respondents spontaneously list items within a given category, commonly used in ethnobotany to identify the most important plants within a specific category (Quinlan 2005). It assumes that people will generally name the species best associated with the said category first and continue listing species in decreasing order of importance. We analysed the free-listing data by calculating the composite salience (CS) values for each species (Smith 1993; Fremout et al. 2021). The CS index indicates the importance of species by considering both the frequency and rank of each species in the free-lists (Smith 1993). The salience of each species in the categories of decomposition and soil fertility was obtained through Eq. 1:

$$CS = \sum_{i=i_1}^{i_N} \frac{\frac{R_i^{-1}}{L_i}}{N} \quad (1)$$

where R_i^{-1} is the species inverse rank in the species list of respondent i. L_i is number of species in the list of respondent i, and N is number of informants. The CS was obtained by using the AnthroTools package for R (Purzycki and Jamieson-Lane 2017). As farmers were asked to list both positively and negatively perceived species, we calculated a CS index for both types of free-lists, with positive CS values for species perceived to have fast leaf decomposition or positive effects on soil fertility, and negative CS values for species perceived to have slow leaf decomposition or negative effects on soil fertility. The 'net CS' of each species was then calculated by subtracting the latter CS value from the former.

All participating farmers, who had between 5 and 60 years experience with agroforestry systems, and pertained to mestizo communities, and 5 out of 46 were women. The questions asked to the farmer were part of a broader set of questions about knowledge and preferences on tree species in cacao agroforestry sytems.

Tree species selection

We selected 15 shade tree species commonly used in cacao agroforestry systems in Colombia, based on their frequency in the visited cacao agroforestry systems while also considering their importance as perceived by farmers in terms of delivery of ecosystem services beyond improving soil fertility (e.g. fruit production, life fence, timber etc., see Table S1). Only species with presence in at least three farms were selected, preferably in different departments. This resulted in the selection of six timber species (*Anacardium excelsum* (Bertero and Balb. ex Kunth) Skeels, *Cariniana pyriformis* Miers, *Cedrela odorata* L., *Cordia alliodora (*Ruiz and Pav.) Oken, *Swietenia macrophylla* King, *Tabebuia rosea* (Bertol.) DC.), three fruit species (*Annona muricata* L., *Persea americana* Mill., *Psidium guajava* L.), one other non-timber species (*Hevea brasiliensis* (Willd. ex A.Juss.) Müll.Arg.), and four nitrogen-fixing taxa (*Pseudosamanea guachapele* (Kunth) Harms, *Bauhinia* L. spp., *Erythrina* L. spp., *Samanea saman* (Jacq.) Merr.) (Table S1). In each location, the leaves of one tree per species were sampled with telescopic scissors, selecting sun-exposed leaves when possible. Each sampled tree at a given farm was the first individual of each species encountered in a variable area transect (Sheil et al. 2003) that was laid out starting from the centre of the farm, in accordance with the project sampling design. We also collected cacao leaves from an additional farm in Santander.

Functional traits

For the 15 shade trees species, functional traits were measured for leaf samples from multiple farms (3 to 9 farms, depending on the species; Table S1). Table 1 lists the functional traits measured, selected for their importance to plant growth (and survival) and leaf decomposition. The traits leaf chlorophyll content (LChlC; SPAD value), specific leaf area (SLA; unitless), leaf nitrogen content (LNC; in %), leaf phosphorus content (LPC; in %), leaf potassium content (LKC; in %), leaf carbon content (LCC; in %), leaf calcium content (LCaC; in %) and carbon-to-nitrogen ratio (C:N-ratio, unitless) (Table 1) were measured in the lab, explained in the paragraph below, while leaf phenology (DCN, deciduous, semi-deciduous, evergreen), nitrogen fixation capacity (NF, yes/no), maximum height of tree (H_{max}, in m) and wood density (WD, in g/cm^3) were derived from the TRY database (Kattge et al. 2020). For cacao, specific leaf area (SLA, petiole included) and chlorophyll content (LChlC) were retrieved from data (leaves from 56 cacao trees) from a study conducted across Peru (Bioversity International, unpublished). Two species were only identified with certainty to genus level (*Bauhinia* and *Erythrina* spp.). To link them to the TRY traits database (Kattge et al. 2020), we used the species names *Erythrina poeppigiana* and *Bauhinia ungulata,* which are most common in Colombia.

Immediately after collecting the branches, the chlorophyll content of four random leaves, from three different branches when in reach of telescopic scissors, was determined in the field with a portable chlorophyll meter (Minolta SPAD-502, Osaka, Japan). The same day of sample collection, photographs were taken of two randomly picked fresh leaves per sampled tree. Leaves were flattened between a plastic panel and a white paper and photographed together with a black square of 36 cm^2. The photographs were analysed with ImageJ 1.53K software (Rasband, W.S. 1997) for obtaining leaf area (in cm^2), using the black square

Table 1 List of functional traits included in this study

Functional trait	Unit	Level of measurement	Method of retrieval
Whole plant traits: morphological			
Nitrogen fixing (NF)	Categorical	Species	TRY Plant Trait data base
Leaf phenology (DCN)	Categorical		
Wood density (WD)	g/cm3		
Maximum height (Hmax)	m		
Leaf traits: morphological			
Specific leaf area (SLA)	$mm^2\ mg^{-1}$	1 individual per species per farm	Dry weight and leaf area of 2 leaves per species per farm
Leaf traits: chemical			
Chlorophyll content (LChlC)	SPAD unit	1 individual per species per farm	4 fresh leaves with SPAD-502 m
Leaf nitrogen content (LNC)	%		Dry combustion analysis on leaf mixture of 1 individual per farm
Leaf phosphorus content (LPC)	%		MEDXRF of leaf mixture of 1 ind
Leaf potassium content (LKC)	%		MEDXRF of leaf mixture of 1 ind
Leaf carbon content (LCC)	%		Dry combustion analysis
Leaf calcium content (LCaC)	%		MEDXRF
Carbon-to-nitrogen ratio	unitless		Dry combustion analysis

as a reference. Two leaves per species per farm were put in envelopes and the remaining leaves were dried in open paper bags before transport. Once in the lab, the leaves were dried at 60 °C for 24 h and the dry weight of the two leaves in the envelopes was recorded. Specific leaf area was determined by dividing leaf area by leaf dry weight.

For the leaf element composition analysis, cacao leaves were also included, using sun-exposed leaves from multiple plants (leaves were mixed) an additional farm in Santander. Therefore, a total of 77 leaf samples from 16 tree species including cacao were analysed. Between 10 and 25 g of each leaf sample were ground using a mechanical grinder to a size of 0.5 mm to create a homogeneous powder. Organic carbon (C), nitrogen (N) and hydrogen (H) (all in %) were determined using dry combustion analyses (Carlo Erba N/C 1500 (Milan, Italy)) using a known weight of leaf sample. The elements P, Ca, and K (in ppm) were measured with the Monochromatic Energy Dispersive X-ray Fluorescence (MEDXRF) method using the E-max Portable Heavy Metal Analyzer for Soil and Food (Z-Spec, East Greenbush, NY, USA) following the protocol described in Dekeyrel et al. (2024).

Leaf decomposition

In the leaf decomposition experiment, three samples (each from different farms) were used of each of the 15 shade tree species, as well as cacao leaves from an additional farm in Santander. For shade tree species sampled on more than three farms, three of those samples were randomly picked (stratified per region). Leaf decomposition was investigated ex-situ in a common garden decomposition experiment. By quantifying leaf decomposition of different species under the same conditions, this method can provide a meaningful comparison of species-specific, functional trait-dependent differences in decomposition rates (Schwinning et al. 2022). The common garden experiment was carried out in the cacao germplasm collection of AGROSAVIA, Palmira (Figure S1), where the shade tree *Samanea saman* was intercropped with cacao. Each 4 rows of 6 cacao trees were surrounded by 4 trees of *Samanea saman*, thereby creating a homogenously shaded understory. This uniform, single-species canopy layer allowed us to control for effects of variation in species identity on leaf decomposition. The location has an average yearly temperature of 23.6 °C and an annual precipitation of 1462 mm (Fick and Hijmans 2017). No pruning of cacao trees took place during the experiment.

Three nylon mesh bags per species per farm (9 litterbags per species) were filled with leaves for retrieval at different points in time. A known amount of ~5.0 g of oven-dried leaves (at 60 °C for 24 h) was put (and when needed folded) into 20 × 15 cm white nylon bags with a 2 mm diameter mesh size, allowing micro- and meso-fauna to access while minimizing leaf loss by pieces falling out of the bags. The 144 bags (16 species × 3 farms (or triplicates in case of cacao) × 3 collection times) were placed in a random order around several cacao trees, at 20 cm from the stem and 15 cm apart from each other. Randomization was implemented by mixing the litterbags in two boxes, from which bags were drawn one at a time and placed in the field in that order. The herb layer and fallen leaves were gently put aside, and the bags were placed on top of the soil in between litter of *Theobroma cacao* and *Samanea saman*.

To estimate the decomposition rates, dry leaf weights of each bag were measured before the experiment, as well as at the time of retrieval of each of the bags, i.e. at three points in time at intervals of approximately 5 and 8 weeks (at t = 39, 95, 133 days). The timing of these intervals was informed by previous decomposition studies, in which significant leaf weight losses were observed after one to three months (Bai et al. 2022; Castillo-Figueroa et al. 2025; Saj et al. 2021). The samples were retrieved carefully from the soil, minimising loss of leaf particles by putting the nylon bag directly in a paper bag. In the lab, the leaf material was separated from the nylon bag and soil, and ants were gently removed with a soft brush. All the leaf material was put in a paper bag in the oven for 24 h at 60 °C. After weight stabilisation, the remaining leaf material was weighed. The loss of dry mass (%) was calculated from initial converted oven-dry weight and remaining oven-dry mass. With the three weight data points, a leaf-mass loss curve was created for each species from three different farms. Decay constants were calculated using the negative exponential decay model of Olson (Olson 1963), using Eq. 2:

$$\frac{Wt}{W0} = e^{-kt} \tag{2}$$

where Wt is the weight remaining at time t, W0 the initial weight, exp the base of natural logarithm, k the decay rate coefficient and t the time in days. The decay constant reflects the rate at which leaves decompose, with a unit of 1/day. Three decay rates per species were calculated (except for the leaves of *Swietenia macrophylla* from one farm, as one litterbag was lost and one showed an increase in leaf weight). The leaf decay rates from three farms were considered as three replicates for each species and averaged for graphically displaying decomposition per species. A linear model was fit with an intercept of zero (Eq. 3), in which the fitted slope of the linear model is equal to the decay constant k.

$$lm(\log(Wx) \sim 0 + tx) \tag{3}$$

Statistical analysis

All data processing and statistical analyses were executed in the R programming environment version 4.2.1 (R Core Team 2022), unless specified otherwise. Relationships between functional traits and microelements were investigated using a correlogram (corrplot package; (Taiyun Wei and Viliam Simko 2021). To further explore functional trait covariation patterns and explore the position of species in functional trait space, a principal component analysis (PCA) was performed with data from all shade tree individuals and cacao. All variables were scaled prior to analysis. We constructed linear mixed effect models to examine which leaf functional traits of shade tree species best explain leaf decomposition. Here, the decay constant k was used as the dependent variable, as it reflects decomposition and showed a significant correlation with leaf dry weight mass loss (see Supplementary Materials S1). We considered the following fixed effect variables: specific leaf area (SLA), leaf carbon content (LCC), leaf nitrogen content (LNC), leaf phosphorus content (LPC), leaf potassium content (LKC), leaf chlorophyll content (LChlC), leaf calcium content (LCaC) and leaf carbon-to-nitrogen ratio (CN-ratio), whereas species were included as a random effect variable (lmer package; (Bates et al. 2015)). Prior to the model construction, all variables were scaled to obtain comparable effect sizes. In the final model, we used the natural logarithm of the decay constant to ensure compliance with model assumptions (Zuur et al. 2009).

The full model of decay k, with 8 leaf traits as predictors, was checked for multicollinearity with a stepwise variance inflation factor (VIF) procedure using

the car package (Fox and Weisberg 2019), resulting in the removal of CN-ratio as predictor variables. Model residuals were checked for normality and heteroscedasticity. Block effects in the experimental set-up were assessed by including the identity of the tree under which litter bags were placed as a random factor, but this was not found to be significant. Also, one-way interactions between variables were tested but found not significant ($p < 0.05$). Also considering the absence of strong hypotheses on specific variable interactions, interactions were not included in Eq. 4. Then, all possible combinations of the fixed effects were made, limited to a maximum of four terms in each model, using the dredge function (MuMIn package; Barton 2023) using Eq. 4:

$$decayk \sim LNC + LKC + LPC + SLA + LChlC + LCaC + LCC \quad (4)$$

All models were assessed using the second-order Akaike Information Criterion (AICc). Only models with an AICc value within 2 units of the lowest AICc (i.e., $\Delta AICc \leq 2$) were selected for model averaging and to obtain the marginal and conditional R2 values (Nakagawa and Schielzeth 2013). These models were then combined using their AICc weights to obtain a single averaged estimate (Burnham and Anderson 2004). Both full and conditional model averaging was then applied to identify the most important variables.

To investigate alignment of farmer perceptions on decomposition and soil fertility improvement with the findings of the leaf decomposition experiment, we calculated correlation coefficients between the corresponding CS values and the decay rate values (k) from the exponential decay curves, averaged per species, as well as the correlation coefficients between the CS values and leaf nitrogen, potassium and phosphorus (i.e. the three main macronutrients) concentrations. As the residuals of linear regressions were not normally distributed, we used the Spearman rank correlation test.

Results

Functional traits of shade trees in cacao agroforestry

The first axis of the species in functional trait space (explaining 34.8% of variation, Fig. 1) reflected the

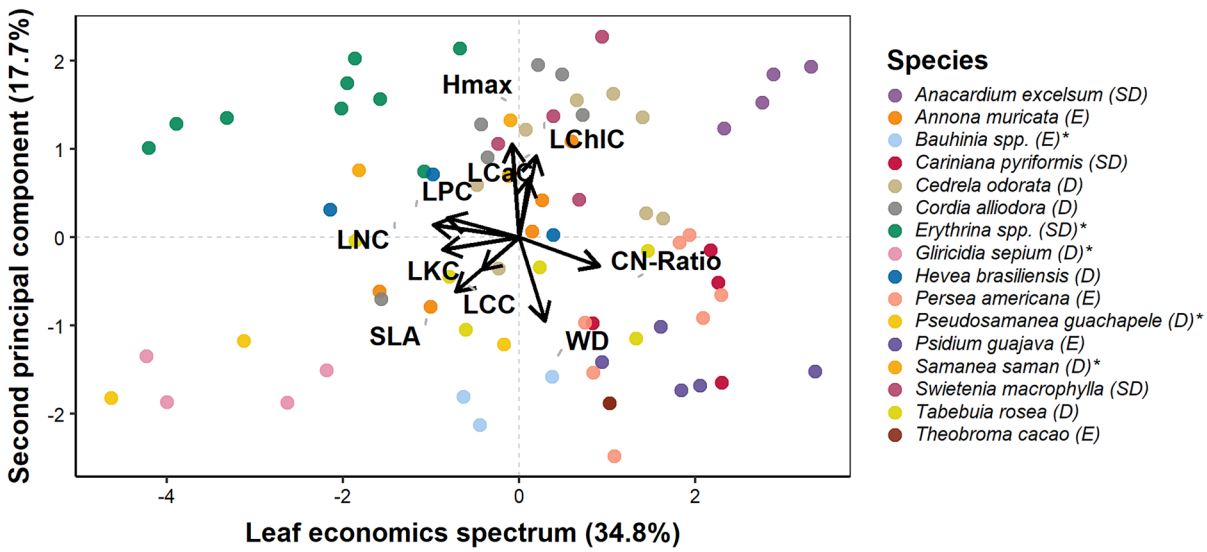


Fig. 1 Biplot of principal component analysis (PCA) of species-averaged leaf and whole plant tree traits for the 15 shade tree species and cacao (*Theobroma cacao*). The functional leaf traits are specific leaf area (SLA, $mm^2\ mg^{-1}$), leaf carbon content (LCC, %), leaf nitrogen content (LNC, %), leaf phosphorus content (LPC, %), leaf potassium content (LKC, %), leaf calcium content (LCaC), leaf carbon-to-nitrogen ratio (CN-ratio) and the chlorophyll index value (LChlC). The whole plant/stem traits are wood density (WD) and maximum potential height (H_{max}). Species leaf phenology is indicated within brackets behind the species names (D: deciduous, SD: semi-deciduous, E: evergreen), and nitrogen-fixing species are indicated with an asterisk (*)

spectrum from high leaf nutrient contents (nitrogen (LNC), phosphorus (LPC) and potassium concentrations (LKC), and high specific leaf area (SLA) on the one end, and high leaf carbon-to-nitrogen ratio (CN-ratio) on the other end (Fig. 1). This represents the leaf economics spectrum, with species with resource-acquisitive strategies located on the negative side (high LNC, LPC, LKC, and SLA) and those with more conservative strategies (high CN-ratio) towards the positive side. Nitrogen fixing species, and to a lesser extent deciduous species were also found mainly on the negative side of PC1. The second axis (explaining 17.7% of variation) reflected the spectrum from tall trees on the one end and high wood density (WD) on the other end, mainly representing the whole plant trait spectrum, though the positive side of the axis was also correlated with high leaf chlorophyll content (LChlC) and high leaf calcium content (LCaC). The species-averaged values of all traits are provided in Table S3, and a correlogram showing the correlations between these traits is shown in Figure S2.

Leaf decomposition of tree species and leaf functional trait predictors

The weight loss over time (Fig. 2A) and the obtained decay constant k per species per farm (Fig. 2B) differed between species and within species between farms. *Gliricidia sepium* showed the highest decomposition rate, followed by *Pseudosamanea guachapele* and *Tabebuia rosea*, whereas the leaves of *Bauhinia* spp., *Persea americana* and *Theobroma cacao* showed the lowest decay rates.

Present in all models with $\Delta AICc \leq 2$, LNC was the best predictor of leaf decay rate k ($p = 0.01$ in both full and conditional average model, Fig. 3).

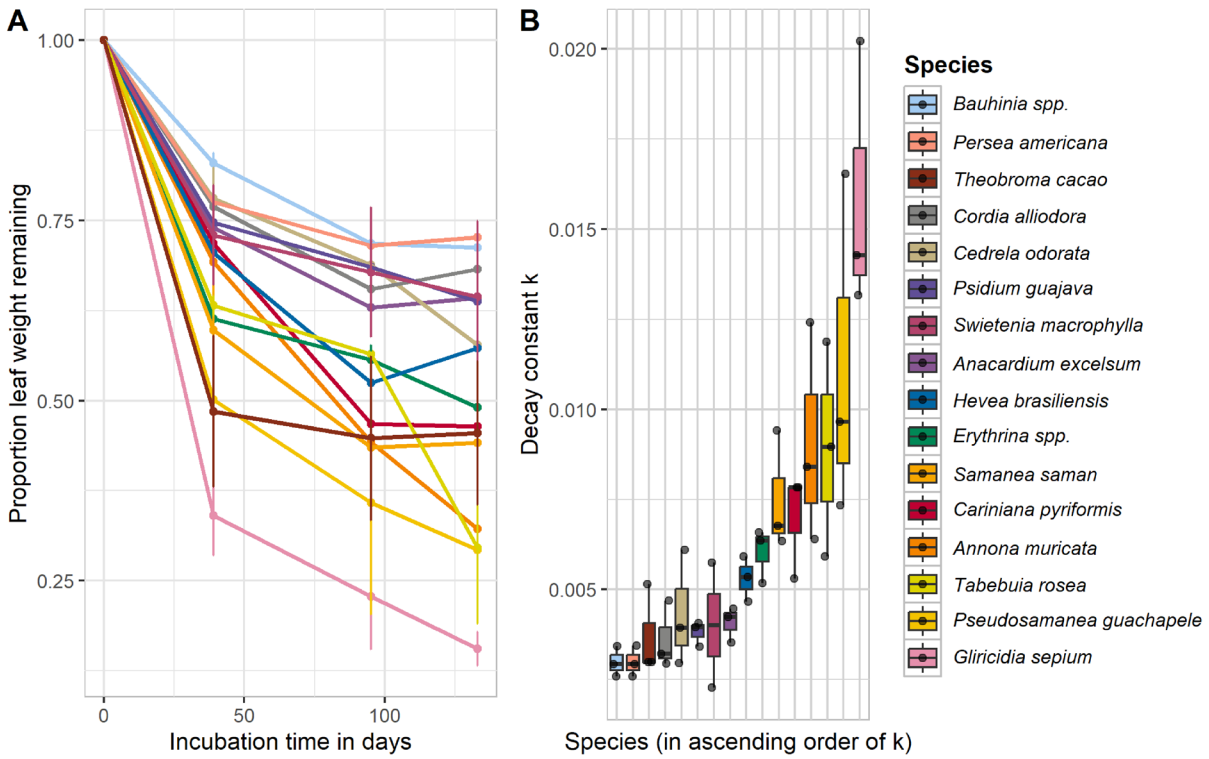


Fig. 2 Leaf weight remaining and decay constants for all species in the common garden experiment. Panel A shows the proportion of leaf weight remaining (0–1) over time (days) (n=3 at each time point, dots represent the average values and error bars represent the standard deviation). Panel B shows the decay constant k for each species, ordered from lowest to highest median value; higher k indicates faster decomposition. Species in the legend are listed from low (top) to high (bottom) median k

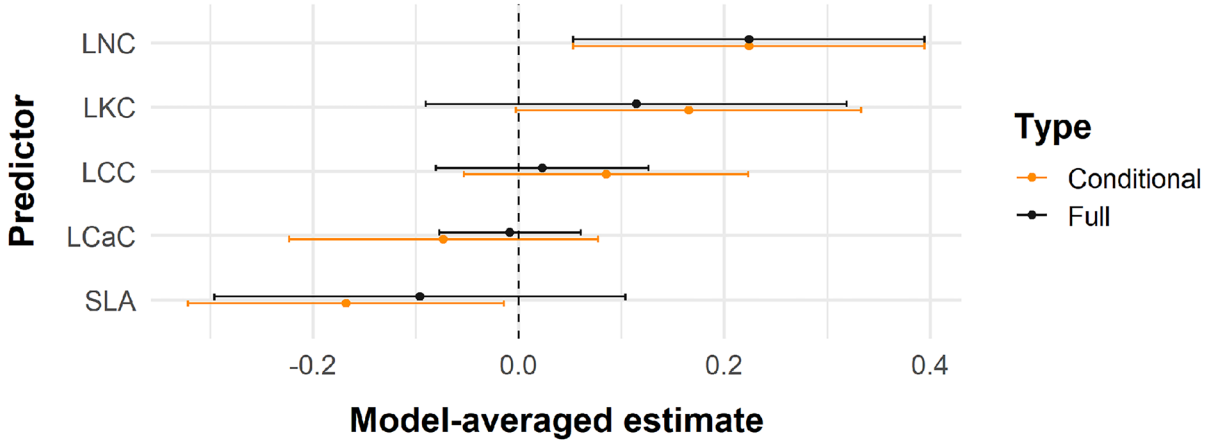


Fig. 3 Predictors of leaf decomposition: model-averaged coefficients (±95% confidence intervals) from linear mixed models with the logarithmic decay constant (*k*) as the response variable. LNC stands for leaf nitrogen content, LKC for leaf potassium content, LCC for leaf carbon content, LCaC for leaf calcium content, and SLA for specific leaf area. Note that LNC was included in all selected models and that therefore the estimates of the conditional and full average model are equal

The conditional average also showed high SLA to be negatively associated with leaf decay ($p = 0.03$) while a high LKC, similar to LNC, predicted a high leaf decay ($p = 0.05$). The marginal R^2 of the six models with $\Delta AICc \leq 2$ ranged from 18.4% to 33.8%, whereas the conditional R^2 ranged from 72.7 to 78.4% (see Table S4).

Local ecological knowledge

The participating cacao farmers listed the shade tree species *Cedrela odorata*, *Erythrina* spp., *Pseudosamanea guachapele,* G*liricidia sepium*, *and Samanea saman* as those with fastest leaf decomposition (Fig. 4A). The same five species formed the top-5 species identified as those with most favourable effects on soil fertility, although in a different order (Fig. 4B). *Anacardium excelsum, Persea americana* and *Bauhinia* spp. were listed as the species with slowest decomposition, whereas *Cordia alliodora*, *Anacardium excelsum* and *Bauhinia* spp. were listed as the least suitable species to improve soil fertility.

Decay rates were positively correlated with species' composite salience (CS) scores expressing local shade tree preference for decomposition ($p = 0.05$). The same CS scores were also statistically significantly ($p < 0.05$) correlated with LNC and LPC. Species preferences for improving soil fertility were significantly correlated ($p < 0.01$) with decay rates (Table 2).

Discussion

Here we present the results of a common garden experiment to investigate differences in leaf decomposition between 15 shade tree species commonly used in cacao agroforestry systems across Colombia. Our results revealed a range of leaf decomposition rates, mostly explained by leaf nutrient contents, largely consistent with farmers' local ecological knowledge (LEK).

Leaf functional traits of shade tree species in cacao agroforestry systems reflect leaf economics spectrum

Among the studied functional traits, leaf nitrogen (LNC), potassium (LKC) and phosphorus (LPC) content and to a lesser extent specific leaf area (SLA) were negatively correlated to the first principal component, where carbon-to-nitrogen ratio (CN-ratio) was positively correlated with these traits. The correlation of these leaf traits constructs the leaf economic spectrum (LES), the second most important dimension in the spectrum of plant form and function, after the dimension of height and diaspore mass, which are negatively correlated across plant species globally (Díaz et al. 2016). The leaf nutrient traits and SLA were associated with tree species' ability to fix nitrogen, which is consistent with the hypothesis that nitrogen fixation reduces

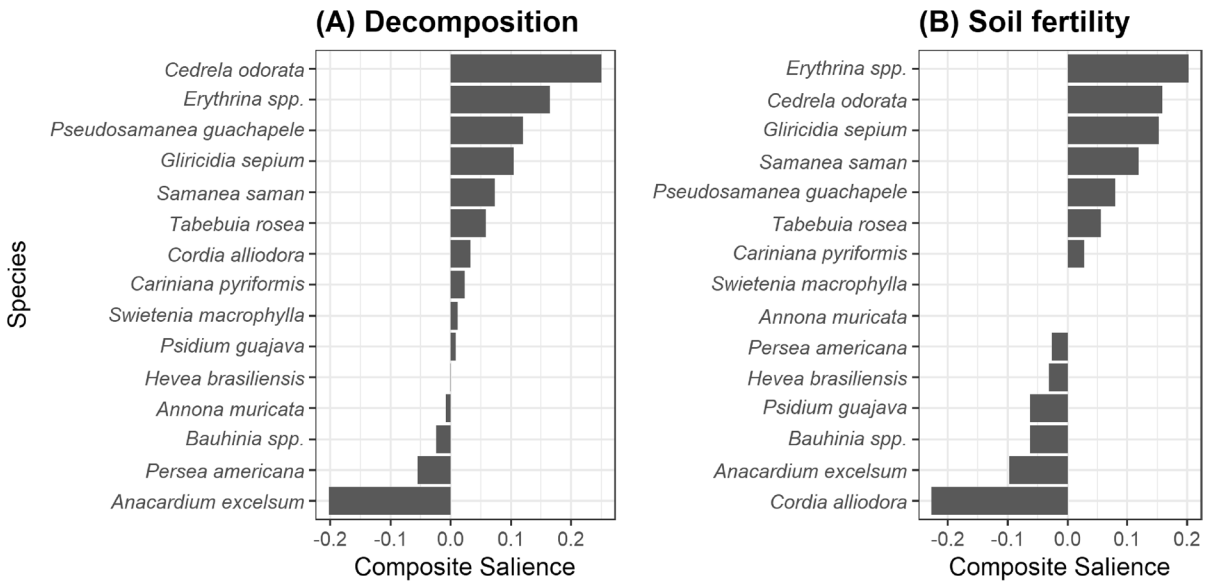


Fig. 4 Composite salience (CS) values of the shade tree species expressing perceived leaf decomposition rates (panel A; more positive CS values correspond to quicker decomposition) and perceived effects on soil fertility (panel B; more positive CS values correspond to more positive effects). Note that farmers also listed other species but that only species used in the decomposition experiment are shown

Table 2 Correlation between farmers' perceptions on the effects of tree species on leaf decomposition and soil fertility versus experimental results: Spearman's rank correlation coefficients between species' composite salience (CS) values and species-averaged decay rates and leaf nutrient contents. *P*-values ≤ 0.05 and $p \leq 0.1$) are indicated with asterisks (*) and dots (·)

Experimental results	Farmer local ecological knowledge	
	Decomposition	Soil fertility
Decay rate k	0.518 ($p = 0.05$) *	0.657 ($p < 0.01$) *
Leaf nitrogen content (LNC)	0.582 ($p = 0.03$) *	0.444 ($p = 0.10$) ·
Leaf potassium content (LKC)	0.504 ($p = 0.06$) ·	0.415 ($p = 0.12$)
Leaf phosphorus content (LPC)	0.611 ($p = 0.02$) *	0.438 ($p = 0.10$) ·

nitrogen limitations in their soil and thereby enables higher leaf nutrient concentrations.

Wood density (WD) was negatively associated with maximum height (H_{max}) and leaf chlorophyll content (LChlC), all correlating with the second principal component. In this study, the whole plant traits WD and H_{max} were not closely associated with the leaf economic spectrum and poor predictors of leaf nutrient contents and leaf decomposition. The decoupling of whole plant traits and leaf traits has been observed in neotropical trees (Baraloto et al. 2010) and Amazonian tree species (Vleminckx et al. 2021). Comparable large-scale trait studies in agroforestry systems are currently lacking, making it difficult to assess whether tree species used in agroforestry also follow these patterns. This decoupling nonetheless contrasts with studies that revealed a whole-plant economic spectrum in subtropical woody species (Li et al. 2022). In contrast to leaf CN-ratio, leaf carbon content (LCC) did not correspond with the two most important axes. (Poorter et al. 2009) noted that carbon is also present in non-structural leaf compounds,

a high LCC therefore does not necessarily represent a conservative resource use strategy, which is in line with our findings.

Leaf decay rates increase with leaf nitrogen content

We hypothesized that functional traits expressing an acquisitive resource use strategy would be indicative of their leaf decomposition rates. Our findings confirm those of other studies that have put forward LNC as the main driver of decomposition (Bakker et al. 2011; Bai et al. 2022; Khulpu et al. 2025; Castillo-Figueroa et al. 2025), although LNC correlated strongly with other leaf nutrient contents (P and K), which are not always considered in other studies (Freschet et al. 2012; Wartenberg et al. 2017; Ristok et al. 2019; Rawat et al. 2020; Wang et al. 2022). While these findings can be used to select species likely to contribute higher amounts of nutrients to the soil based on how quickly their leaves decompose, we must consider the role of species identity and unmeasured traits. The relatively large difference between the conditional and marginal R2-values suggests that a considerable part of the variation in leaf decomposition rates can be explained by species identity and possibly interspecific differences in leaf functional traits that were not measured, such as leaf lignin content (Freschet et al. 2012; Qu et al. 2019), leaf tannin content (Ristok et al. 2019; Zhao et al. 2022) or leaf mechanical properties (Bakker et al. 2011; Li et al. 2023; De Alencar et al. 2024).

Unexpectedly, SLA was a negative predictor of leaf decomposition, although not significant in the full model average. While this relationship should therefore not be over-interpreted, this may suggest that leaf nutrient contents are more important than leaf structure in determining leaf decomposition. It might also be related to the use of samples with equal weights across all species, as this resulted in higher number of leaves per mesh bag for high-SLA species, causing these samples to be more squeezed and potentially reducing the contact area with decomposers, slowing down decomposition. While some studies have found leaves with a high SLA to decompose faster (Cornwell et al. 2008; Bakker et al. 2011), other decomposition studies reported no effect of SLA (Freschet et al. 2012; Jo et al. 2016; Pichon et al. 2019; Rawlik et al. 2021).

Integration of traditional and scientific knowledge central for adaptive learning and stewardship

The experimental decay rates of the 15 shade tree species correlated with farmer knowledge on the best species to improve soil fertility ($p < 0.01$) and decomposition ($p = 0.05$). Species whose leaves were said to decompose fastest according to farmers also had higher LNC ($p = 0.03$) and LPC ($p = 0.02$). Our finding that species perceived as most suitable for improving soil fertility were less strongly correlated with leaf nutrient contents may be because farmers' appreciation of a species contribution to soil fertility covers notions that go beyond leaf characteristics. Traits such as root architecture, canopy structure, water retention capacity (Xing et al. 2024), but also nutrient uptake rates or nutrient inputs through falling flowers and fruits can all influence farmer judgements. Most importantly, these findings underline that farmer knowledge is a valuable source of information to select tree species in cacao agroforestry systems, complementing knowledge from experimental studies and global plant trait databases. Although relatively few studies have attempted to explicitly integrate local knowledge with scientific findings, existing examples (Jacobi et al. 2017; Velázquez-Rosas et al. 2018; Isaac et al. 2018; Fremout et al. 2021; Magalhães et al. 2021; Bourne et al. 2023) highlight the great potential of combining both sources of knowledge to inform locally adapted agroforestry design and management.

Tree species choices by farmers are influenced by multiple factors, among which ability to enhance soil fertility is only one element, and generally preferred species fulfil multiple functions simultaneously (Pauli et al. 2012). Hence, tree species that provide multiple benefits in terms of services (e.g., erosion control, soil fertility, disperse shade), food security or income generation, and are easy to manage (e.g., in terms of propagation, pruning) have a higher chance of being adopted by farmers (Fig. 5). Agroforestry practices are only sustainable if implemented with stewardship over the long term (Cerdán et al. 2012; Ollinaho and Kröger 2021). Therefore, tree species recommendations should not only coincide with efforts to improve nutrient status or be solely based on experimental findings (Ollinaho and Kröger 2021), but also consider the knowledge and the needs of farmer households (Groot et al. 2012;



Fig. 5 Vegetatively propagated *Erythrina* sp. tree in a cacao agroforestry plot affected by gully erosion, frequently and heavily pruned for increasing soil fertility and reducing soil erosion

Van der Wolf et al. 2019). When tree species recommendations are rooted in local knowledge and preferences, not only will they be more useful for local farmers, but they are more likely to be adopted (Blay et al. 2008). To facilitate sustainable integration of local and scientific knowledge, one could consider methods such as "dialogo de saberes" (Martínez-Torres and Rosset 2014; Magalhães et al. 2021), co-production methods (Bourne et al. 2023) and boundary work (Clark et al. 2016), among others. In conclusion, two-way dialogue and knowledge exchange between farmers, technical support staff and scientists is pivotal, not merely to validate either source of knowledge, but to promote adaptative learning and encourage socio-ecological stewardship (Jacobi et al. 2017; Misanya et al. 2023).

Both the LEK and experimental findings of this study were integrated in the online cacao agroforestry co-design tool Diversity for Agroforestry (D4A; www.diversityforagroforestry.org), to support future decision making. The D4A tool recommends tree species for integration in agroforestry systems based on functional trait data as well as local knowledge of cacao farmers to match species with tree planting objectives, among which is the improvement of soil fertility.

Implications for improving nutrient cycling in cacao agroforestry systems

This study highlights the importance of resource-acquisitive tree species with nutrient-rich leaves in cacao agroforestry for increasing leaf decomposition rates. Cacao leaves themselves have a high C:N ratio and decompose slowly, which can aid in protecting soil moisture, stable soil temperature and structure as well as assisting in more asynchronous nutrient release when mixed with low C:N leaves (Bai et al. 2022). In line with Sauvadet et al. (2020), our findings emphasize the potential of incorporating trees with dissimilar traits to cocoa (i.e. resource-acquisitive traits) for improving litter decomposition. Among resource-acquisitive tree species, nitrogen fixers are especially promising as they have the potential to increase nitrogen inputs through their residues, including prunings (Hartemink 2005; Kähkölä et al. 2012; Schneidewind et al. 2019) and root residues (Kähkölä et al. 2012), with potential positive effects on cacao productivity, even at close distances between shade trees and cacao plants (Notaro et al. 2021). This is especially critical for farms under organic management (Sauvadet et al. 2019) or with degraded soils with low organic matter and associated nutrient stocks.

As cacao seeds are high in potassium (K), repeated cacao harvests can drastically reduce cycling and availability of this nutrient (Hougni et al. 2021), as illustrated by a nutrient off-take model for cacao in Africa (Vasquez-Zambrano et al. 2025). Consequently, cacao agroforestry systems are often K-limited (Hartemink 2005; Sujatha and Bhat 2013; Mortimer et al. 2018). Our results suggest that such nutrient limitations can be reduced through the strategic use of selected tree species such as the nitrogen-fixing species *Gliricidia sepium* and *Pseudosamanea guachapele,* whose leaves had the highest levels of K content (Table S3), in line with findings of Bai et al. (2022). However, we do not claim that all nutrient limitations in cacao production can simply be overcome through intercropping with trees. To enhance

productivity of smallholder cacao systems, the balanced use of external nutrient inputs from organic and/or synthetic sources remains important in most contexts (Hougni et al. 2021; Vasquez-Zambrano et al. 2025; Sujatha and Bhat 2013).

Besides leaf characteristics, several other factors influence nutrient delivery to the soil through decomposing litter and prunings. Litter decomposition is affected by site-specific conditions such as temperature, rainfall, soil pH and moisture (Hossain et al. 2011; Hougni et al. 2021). The shade generated by the trees themselves alters local microclimates; for example a dense canopy can alter decomposition rates by buffering temperature and moisture extremes, and supporting soil fauna activity (Martius et al. 2004; Köhler et al. 2009; de Carvalho et al. 2021). Also the amount of leaf litter inputs differs between species (Bray and Gorham, 1964) and increases with aboveground standing biomass (Zhou et al. 2007; Lohbeck et al. 2015; Morffi-Mestre et al. 2020). Management practices such as irrigation mitigate drought effects and favour decomposer communities and thereby enhance leaf decomposition (Bakker et al. 2011; Xie et al. 2020) whereas fertilizationmay have similar effects by taking away nutrient limitations, although the effects of fertiliziation on leaf decomposition in agroforestry is not well-studied (Hougni et al. 2021). Pruning can increase and regulate the litter quantity, as well as significantly increasing cocoa yields (Esche et al. 2023). Moreover, fresh leaves have a higher nutrient content than senescent leaves (Killingbeck 1996; Maillard et al. 2015) and have been found to decompose faster (Guo et al. 2024). Therefore, fresh leaves from pruning are expected to increase nutrient flows to the soil in comparison with natural litterfall. In this study, fresh leaves were used, reflecting more realistically the potential effect of pruning on leaf litter decomposition.

Conclusions

Studying the effect of shade trees' functional identity on leaf decomposition addresses an important knowledge gap around nutrient-limited, smallholder cacao agroforestry systems in Colombia and beyond. Based on a common garden experiment, this study revealed resource-acquisitive chemical leaf traits as predictors of enhanced decomposition, underlining the importance of actively pruning resource-acquisitive trees for improving leaf decomposition. Our field data on leaf decomposition supported farmers' shade tree preferences for improving decomposition as well as soil fertility. This puts forward species selection as a key driver of leaf decomposition and soil fertility in cacao agroforestry. We highlight the importance of incorporating local knowledge to improve nutrient cycling and soil fertility, and to motivate cacao farmers to adopt and adapt agroforestry systems.

Future research should combine longer-term, on-farm decomposition studies with assessments of soil biological activity, including both microbial communities and macrofauna (such as ants, termites, and earthworms). Such approaches would help clarify how soil organisms and local site conditions influence leaf decomposition. Studying these dynamics under real farm conditions and over longer time scales will provide a better understanding of how shade tree traits influence nutrient cycling and soil fertility in cacao agroforestry systems. Lastly, future studies on shade tree selection should aim to integrate farmer knowledge to guide participatory hypothesis testing, and align research with farmer needs, interests and realities.

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curation, writing—review and editing; MP: methodology, resources, writing—review and editing, funding acquisition; ET: conceptualization, methodology, writing—review and editing, funding acquisition.

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