



**TROPICAL AGRICULTURAL RESEARCH AND HIGHER EDUCATION CENTER**

**EDUCATION DIVISION**

**POSTGRADUATE PROGRAM**

**Effect of functional diversity on ecosystem services in cocoa agroforestry systems**

**A thesis submitted for consideration by the Education Division and the Postgraduate Program as a requirement to qualify for the degree of**

***MAGISTER SCIENTIAE***

**in Agroforestry and Sustainable Agriculture**

**Cassio Pinheiro Edelstein**

**Turrialba, Costa Rica**

**2023**

This Master's thesis has been accepted in its present form by the Division of Education and the Graduate School Program of CATIE and by the advisory committee of the student, considering that it fills the requirements necessary for the student to present the final defense as well as participate in the final exam

**MAGISTER SCIENTIAE IN AGROFORESTRY AND SUSTAINABLE AGRICULTURE**

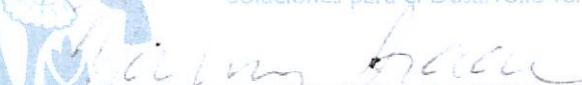
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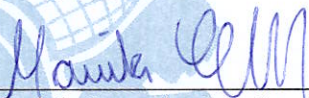
Rolando Cerda Bustillos, Ph.D.  
**Thesis director**



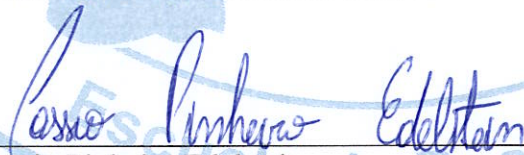
Felipe Peguero Pérez, Ph.D.  
**Member of the Advisory Committee**



Marney E. Isaac, Ph.D.  
**Member of the Advisory Committee**



Mariela Leandro Muñoz, Ph.D.  
**Dean, a.i., of the Graduate School**



Cassio Pinheiro Edelstein  
**Candidate**

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## List of acronyms

AFS: Agroforestry system  
 AGB: Aboveground biomass  
 AFS: Agroforestry system  
 DBH: Diameter at Breast High  
 ES: Ecosystem services  
 FD: Functional diversity  
 FT: Functional traits  
 LDMC: Leaf dry-matter content  
 LNC: Leaf Nitrogen Concentration  
 LPC: Leaf Phosphorus Concentration  
 N:P: Leaf Nitrogen and Phosphorus Concentration ratio  
 Hmax: Maximum vegetative high  
 SLA: Specific Leaf Area  
 LA: Leaf area  
 SLW: Specific Leaf Weight  
 SSD: Specific stem density  
 FDis: Functional dispersion  
 Rao's Q: Quadratic Rao

## **Acknowledgements**

I would like to acknowledge the support of the Latin-American Model Forests Network, the Government of Canada, and the Forests and Biodiversity in Productive Landscapes Unit of CATIE for providing the scholarship opportunity. My gratitude also extends to the Ministry of Agriculture of Costa Rica and its staff—Rocío Fallas, Kennet Bolivar, Jimmy Medina, Daniela Mora, and Ányelo Moya—for their assistance in identifying the studied population.

I want to express my gratitude to Dr. Rolando Cerda for his dedication as a teacher and advisor, guiding me through the science of agroforestry systems. I extend my appreciation to Dr. Marney Isaac for her significant contributions to the development of functional diversity research in agroecosystems and for sharing her experience in advising me. I am also thankful to Dr. Felipe Peguero for his academic guidance and personal advice.

Acknowledgments to the Forests and Biodiversity in Productive Landscapes Unit of CATIE for their support in tools and leaf sample collection. Thanks to Dr. Bryan Finegan for his assistance in understanding functional diversity, Diego Delgado for introducing me to the field, and Leo Coto for practical recommendations in leaf sample collection.

I am grateful to Fernando Casanoves, Sergio Vilchez, and Eduardo Corrales from the Biostatistics Unit of CATIE for their support and guidance.

Lastly, special thanks to Jeison Salazar for his valuable field assistance.

## 1. Resume

Cocoa agroforestry systems provide multiple ecosystem services (Cerdeira et al. 2014; Somarriba et al. 2013; Isaac et al. 2007), which can be assessed through functional diversity to support agricultural management (Díaz et al. 2007, Martin y Isaac 2015). In this research, carried out in one of the largest cocoa-producing regions in Costa Rica, functional trait ecology was applied to understand clonal cocoa Agroforestry Systems (AFSs) dynamics by analyzing the effect of functional diversity on three ecosystem services: carbon storage, nutrient fertility, and provisioning of cocoa and other products. We characterized the functional diversity of cocoa AFSs across a gradient of ecological complexity and established relationships between functional diversity indices and ecosystem services. Two contrasting ecological dynamics were observed; the low complexity AFSs were characterized by the dominance of resource-conservative traits (higher *leaf dry matter content*, LDMC, higher *stem specific density*, SSD, and low *leaf nitrogen concentration*, LNC) and were associated to lower carbon stocks and lower soil chemical fertility, in contrast to the most complex AFSs, that presented resource-acquisitive traits (low LDMC, low SSD and high LNC) (Garnier et al. 2004) and produced more ecosystem services. The functional diversity was further instrumentalized to a functional-based management by analyzing the relationships between effect and response traits in connection with ecosystem services, including cocoa yield, and providing evidence of the most important functional traits driving specific ecosystem services and multiple ecosystem services in cocoa AFSs. Shade canopies composed by tree species with high Hmax, high LNC, low LDMC, low *specific leaf weight* (SLW), and low *leaf nitrogen-phosphorus ratio* (N:P) enhanced carbon storage, soil fertility, and multiple ecosystem services, while the cocoa yield responds to soil potassium content and to the management of shade percentage, especially from large leaf shade trees.

Key-words: Agroecology; Agroecosystem; multifunctional agriculture; sustainable agricultural intensification; clonal cocoa; functional ecology; functional trait; multistrata agroforestry systems.

## 2. Introduction

Agroforestry Systems (AFSs) are characterized as an agricultural technique that involves multiple species in the same area, with at least two components that interact with each other and at least one woody perennial species (Somarriba 1990, Torquebiau 2000). Therefore, as a science, agroforestry branches from agronomy and forestry. However, it diverges from both subjects because of its inherent complexity involving the interactions between multiple species.

The common agronomical approach projects the crop performance as an outcome of the crop species and variety, environmental conditions, and management practices (Martin y Isaac 2015). Another component of biodiversity, the functional diversity, allows to project the performance of a whole plant community with diverse species based on the functional traits of its individuals (the ecophysiological characteristics that affect species-ecosystem interactions) and how these functional trait values vary, generating ecological processes such as better exploration of the ecosystem resources, resilience, or low differentiation and competition (Martin y Isaac 2015, Violle et al. 2007, Tilman 2001).

Functional ecology characterizes plants based on their function rather than their taxonomic identity. This approach reduces the vast array of species to a more manageable set of variables known as functional traits. These traits, measurable in all plants, allow for the creation of scales to quantify and compare species functions. In turn, this facilitates the calculation of interspecific and intraspecific species interactions. By emphasizing ecological processes arising from interconnected components within a system, functional diversity plays a crucial role in unraveling the complex chain of interactions inherent in multiple species consortia (Pla et al. 2012), which are intrinsic to AFSs.

Functional diversity can also be applied in order to understand the relationship between community compositions and ecosystem services in agroecosystems, because the functional traits of plants carry strong relationships with ecological properties and processes related to carbon sequestration, nutrient cycling, water availability, among others (Casanoves et al. 2011, Lavorel y Garnier 2002, Díaz y Cabido 2001, Funk et al. 2017).

Previous studies have compared AFS plots with varying species richness and tree densities, revealing a noteworthy impact of these biodiversity variables on productivity and the provision of ecosystem services (Cerda et al. 2014). Meanwhile, other research has identified a threshold. Beyond this threshold, increases in these biodiversity components continue to enhance ecosystem services but lead to a negative tradeoff with productivity (Cerda et al. 2014; Blaser et al. 2018).

Authors who have examined functional diversity in AFSs have noted that the functional traits of shade trees can elicit diverse effects on environmental conditions (Gagliardi et al. 2021). These traits play a role in shaping microclimates, affecting the development of pests and diseases, influencing weed suppression, and impacting crop yield (Gagliardi et al. 2021; dos Santos et al. 2021). This unveils a novel functional-based approach for analyzing, planning, and managing AFSs (Martin and Isaac 2015).

Agroforestry systems with clonal cocoa varieties are resistant to diseases and achieve higher productivity, which is why it is expected that the number of producers adopting these improved genetics will continue to grow. Therefore, is important to study the biological interactions in clonal cocoa plantations, in order to support a sustainable agricultural intensification with more biological diversity and ecosystem services generating positive externalities.

To evaluate the application of functional diversity in agroecosystems, this research quantified and characterized the functional diversity and the ecosystem services of cocoa AFSs on contrasting

ecological conditions, from simple to highly biodiverse systems, and analyzed the effect of functional diversity on the production of ecosystem services of provisioning (yield of cocoa and other products), regulation (carbon storage), and support (nutrient fertility).

## 2. Methodology

### 2.1 Strategy for sampling cocoa farms

To analyze the effect of FD in ecosystem services along a gradient of ecological complexity, we selected cocoa AFS plots with different levels of ecological complexity, which was assessed using species richness, a traditional biodiversity proxy (Moreno-Mateos et al. 2020).

Species richness serves as a suitable proxy for defining ecological complexity in this study because it can be visually estimated when comparing AFSs with contrasting conditions, allowing us to select plots with different complexity levels. Moreover, species richness is expected to be correlated to functional diversity (Lawton et al. 1998, Naeem 2002, Tilman 1999). Hence, the variation in species richness across the plots should be mirrored by a corresponding variation in functional diversity, creating a sample with sufficient functional diversity variability to enable the analysis of patterns and trends related to functional diversity through multiple regressions.

Given these considerations, we searched for farms with different levels of species richness, aiming to distribute as much as possible the AFS plots into three groups: the Low ecological complexity group, with 1 to 2 shade tree species, the Medium ecological complexity group, with 3 to 5 shade tree species, and the High ecological complexity AFS group, with more than 6 shade tree species.

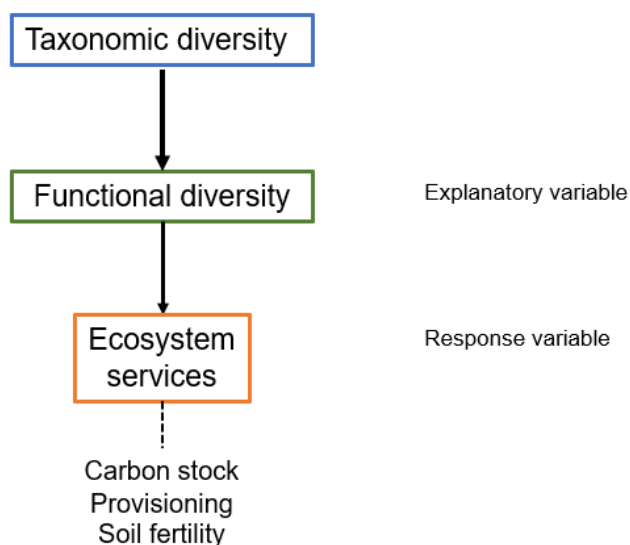


Figure 1: Research design scheme.

To select the cocoa plots, we consulted the data from the cocoa census of Costa Rica from 2020-2021 (Ministerio de Agricultura y Ganaderia, MAG) and filtered among all the cocoa producers from Costa Rica in order to obtain a list of the farms that fit with the following criteria: outside of indigenous territories; only cocoa AFSs (no monocultures); area of cocoa plantation between 0.5 and 14ha; within the age range of 7-20 years; only clonal cocoa AFSs; performing cocoa pruning practices at least once a year; and a yield of at least 100kg of dry cocoa per hectare per year. By applying these criteria, we ensured to select cocoa farms that are active (avoiding abandoned ones) and maintained



relative homogeneity in terms of age and management practices, in order to solely analyze the effect of FD by reducing the interference of other variables which can affect the ecosystem services.

Clarifying the choice of criteria, we excluded monocultures due to the challenge of quantifying FD indices in communities with only one species. The size range was carefully chosen to exclude plots with significantly different management strategies and to avoid the influence of surrounding areas, particularly for very small plots susceptible to external influences (Somarriba et al. 2001). The age range was set to ensure the selection of plots already in cocoa production, with shade trees reaching a sufficient size (more than 5 cm DBH) to be considered in the survey. This ensures that shade trees express traits influencing cocoa performance. Our focus on plantations with regular pruning practices and a production of more than 100 kg of dry cocoa per hectare per year serves as indicators of minimal management conditions. This approach aims to reduce the likelihood of selecting abandoned plantations.

Furthermore, we exclusively analyzed clonal cocoa AFSs due to their proven resistance to Moniliasis and their superior yield potentials compared to traditional local varieties. Therefore, plantations with clonal cocoa shouldn't be compared with traditional cocoa plantations within the scope of this research.

By filtering the cocoa farms from the census through these criteria, were obtained 43 farms from Caribbean Huetar and 19 farms from North Huetar and just a few farms from the Brunca region. This left Caribbean Huetar as the sole suitable region for this research, given its abundance of cocoa farms; it was the only one that surpassed our targeted population size of thirty plots. However, during the field visits we found that only 14 of the 43 farms in the Caribbean Huetar region were actively managing and producing cacao. The majority suffered adverse effects by the Coronavirus pandemic and its impact on the international cocoa market. Consequently, we had to adjust the age criteria, including younger plantations with at least five years. With support from cocoa technicians at the Ministry of Agriculture in Costa Rica (Ministerio de Agricultura y Ganadería, MAG), we employed a chain referral sampling method to identify another 16 farms, to complete all the thirty samples meeting our research criteria. During field visits, one additional criterion was applied to ensure the selection of plots with comparable structure: a minimum of 3 shade trees per plot (equivalent to 30 shade trees per hectare). Finally, after defining all thirty farms for the research, one plot was established in each farm.

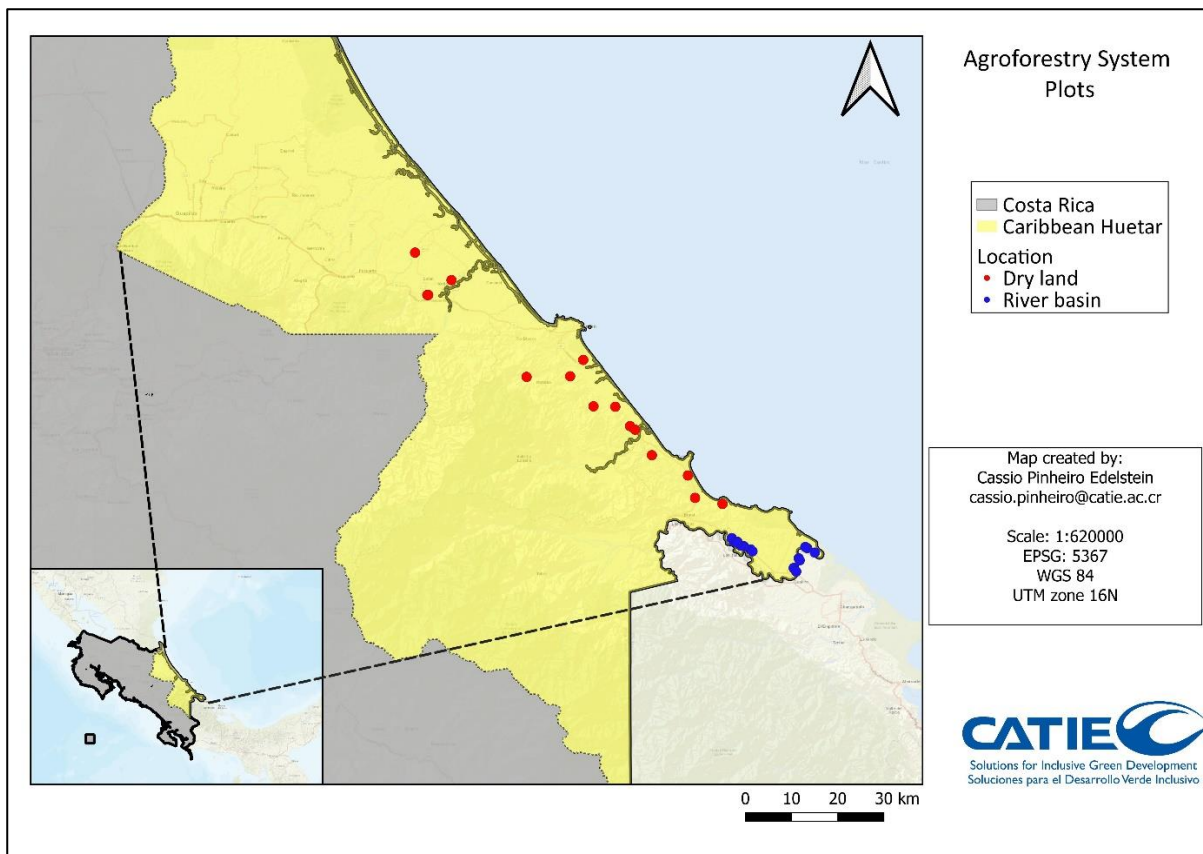


Figure 2: Distribution of the thirty AFS plots in Caribbean Huetar region of Costa Rica. Blue dots indicate plots in the Sixaola river basin and red dots indicate plots outside the Sixaola river basin.

## 2.2 Study site

The Caribbean region has the biggest cocoa production in Costa Rica, and cocoa is fundamental for the economy of many producers, from indigenous communities traditionally growing cocoa in multi-strata highly diverse agroforestry systems (Somarriba et al. 2003) to more intensified productions that use modern and improved cocoa varieties.

The spread of *Monilia* (*Moniliophthora roreri*) affected drastically Costa Rica's cocoa production in the 1970s, and the region went through a process of fast occupation and deforestation from when the extensive cattle farming became the predominant activity in the area (Mantel 1993). Pruning, prevention, and control methods, coupled with the development of cocoa clonal varieties resistant to cocoa diseases and exhibiting higher productivities, have rekindled optimism for cocoa production in Costa Rica (CIC 2018). The sustainable nature of this crop, which can be cultivated in a forest-like agroecosystem with a high diversity of trees, not only generates employment opportunities but also enjoys international recognition for its quality, leading to premium prices. This underscores the significance of Cocoa Agroforestry Systems (CAFS) in contributing to Costa Rica's agricultural objectives (CIC 2018).

Caribbean Huetar Region has a big number of cocoa agroforestry farms with contrasting biological compositions, forming a gradient of complexity across the CAFSs which creates adequate conditions to test the effect of functional diversity on ecosystem services, in addition to the hundreds of shade tree species grown alongside cocoa, banana, annual crops, and secondary forests (Somarriba et al. 2003).

The Caribbean region has a tropical rainy climate, classified as a tropical rainforest climate (Af-climate) according to Köppen (1923), with no distinct dry season and the driest months having more than 60mm of precipitation (Mantel 1993). The annual precipitation varies from 2600mm, in the lower altitudes, to 6400mm, in the higher altitudes (Polidoro et al. 2008). This research only involves plots located in the low altitudes.

The main orders of soils found in the Caribbean region are the ultisoles, inceptisoles and entisoles (Chinchilla Mata et al. 2007).

## **2.3 Field measurements**

### **2.3.1 Characteristics of the plots**

In each cocoa AFS, a representative plot of 1,000m<sup>2</sup> was established, reflecting the overall species richness and structure of the respective farm's AFS. The plot size adhered to a standard recommended for agroforestry investigations (Somarriba et al. 2013, 2001), defined as a rectangle with dimensions 20x50m. Plots were not established on the borders of the plantations, and a minimum density of 30 shade trees per hectare (3 shade trees per plot) was maintained.

To collect soil samples and measure shade, we divided the plot into four subplots by splitting the 50m length into four sections of 12.5m each. These subplots were not treated as pseudo-replicates since they were not utilized for statistical comparisons. The purpose of subdividing the plot was to achieve a more comprehensive representation of the soil and shade by ensuring well-distributed measurements across the plot.

### **2.3.2 Taxonomic identification and measurements of trees**

All woody perennial species with a Diameter at Breast Height (DBH) exceeding 5cm were identified and measured.

The commercial bole height and total height (m) of each tree were measured using a clinometer. For cacao and Musaceae, the height was measured with a graduated rod, while the Diameter at Breast Height (DBH) was measured with a diametric tape at 30cm for *Theobroma cacao* and at 1.3m for all other tree species (Parresol 1999) or over the buttress root when present. Canopy diameter was measured along two orthogonal axes, encompassing the branches that formed the largest diameter.

The data were utilized to calculate species richness (per hectare), relative abundance, shade percentage, functional diversity, and to estimate carbon stocks.

### **2.3.3 Shade percentage**

To control one of the main explanatory variables for understory productivity, we quantified the shade percentage (Blaser et al. 2018).

Shade was measured using HabitApp, a cellphone application designed for shade cover estimation, with prior reports of its successful use in measuring shade percentage in cacao and coffee agroforestry systems (Gerlach et al. 2023; Dainese et al. n.d.). This measurement involved capturing one picture from each subplot, taken from above the cacao canopy, and calculating the average shade percentage.

The HabitApp shade measurement was validated through a linear regression with the results obtained from a classical method (Somarriba 2002) that was also employed. The two methodologies exhibited a significant linear relationship ( $p < 0.05$ ).

The classical method for shade cover estimation involved measuring the shade canopy diameter of all shade trees with a Diameter at Breast Height (DBH) greater than 5 cm. The canopy diameter was determined as the average of two orthogonal axes, encompassing the longer branch. For each of these plants, occlusion was estimated as the percentage of leaves covering the canopy area (Somarriba 2002).

The average canopy diameter (D) of each species is converted to canopy area (A) for the species (equation *i*):

$$(i) A_i = \frac{\pi}{4} * D^2_i$$

The occlusion percentage (o) is multiplied by the canopy area (A) in order to calculate the shade area (ao) of each tree (equation *ii*):

$$(ii) ao_i = A_i * o_i$$

The shade percentage in the plot (S) is calculated as the sum of the occlusion of each tree species multiplied by their respective population (p) (equation *iii*):

$$(iii) S = \frac{\sum(ao_i * p_v)}{100}$$

Where S is the total shade of the whole area; ao<sub>i</sub> is the shade from the i-th tree; p<sub>v</sub> is the population of the same v-th species from the i-th tree.

Finally, S is divided by the plot area and multiplied by 100 to calculate the shade percentage (S%).

We decided to use the HabitApp shade cover results, since we believe that the classical method can overestimate the shade cover in multi-strata AFSs, because of the overlap of tree canopies.

#### 2.3.4 Soil sampling

AFSs can exhibit high variability in microclimate and soil conditions due to their diverse range of species (Gagliardi et al. 2021; Isaac et al. 2007). To collect representative soil samples, each 1,000m<sup>2</sup> plot was divided into four 250m<sup>2</sup> subplots. From each subplot, three soil subsamples were taken: (1) at an intermediate distance between a trunk and the canopy edge of the visually dominant shade species in each subplot (comprising approximately 80% of tree biomass in the plot), (2) 1 m away from the base of a cocoa trunk, and (3) from an area with relatively low tree canopy cover (adapted from Sauvadet et al. 2020) (Figure 2). At each sampling location, one subsample for soil texture and soil chemical fertility was collected at 5-20cm depth using a probe.

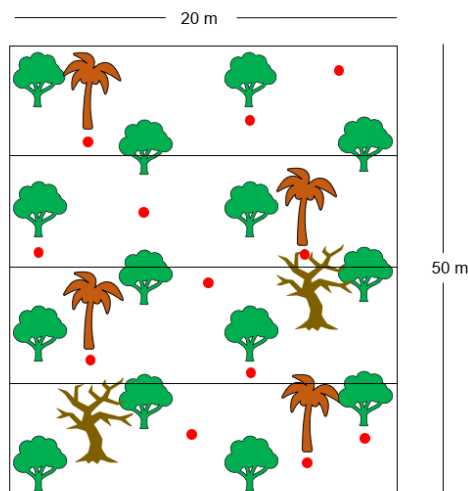


Figure 3: Plot design and example of soil subsamples distribution (red dots).

The resulting 12 subsamples for soil fertility and texture were combined to create one composite sample weighing 400g per plot. This sample was sent to a laboratory for the following analyses: total soil nitrogen content, soil extractable phosphorus, soil extractable potassium, soil extractable calcium, soil extractable magnesium, soil organic carbon content, pH, acidity, and soil texture (granulometry).

The analysis method for total nitrogen and soil organic carbon followed the Combustion Method, utilizing an autoanalyzer. pH was determined using the water method. Calcium, magnesium, and acidity were extracted in potassium chloride (KCl) 1N. Phosphorus and potassium were extracted using the modified Olsen method at pH 8.5.

### 2.3.5 Interview with producers

A semi-structured interview was carried out with producers from the selected farms to capture the age of the cacao plantation, the size of the cocoa growing area, and the estimated cocoa production per year. The complete survey is presented in annex IV.

## 2.4 Methodology to characterize the functional diversity

### 2.4.1 Quantification of functional traits

The functional traits measured were selected *a priori* based on mechanistic criteria well-described in the literature, linking them to the research objectives of analyzing their association with ecosystem services related to primary production, soil fertility, and carbon sequestration (Table 1).

Nine functional traits were assessed: maximum vegetative height (Hmax), leaf area (LA), specific leaf area (SLA), specific leaf weight (SLW), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC), leaf nitrogen and phosphorus concentration ratio (N:P), and specific stem density (SSD).

There is scientific evidence indicating that the selected traits are associated with ecosystem services related to plant productivity, soil fertility, and carbon sequestration (Table 1). These traits can function as response traits, adapting the plant to environmental conditions and regulating its photosynthetic efficiency and resource use efficiency (Smart et al. 2017). Additionally, they can serve as effect traits,

inducing changes in environmental properties by storing carbon and promoting nutrient cycling, for example (Díaz et al. 2007; Finegan et al. 2015; Martin and Isaac 2015).

Provisioning encompasses various aspects related to plant physiology and functional traits. However, since provision can originate from multiple AFS components, the characteristics of the provisioning plant and its derived products may depend on different plant strategies and traits. For example, a timber tree with high density may exhibit longer durability and higher commercial value, while a tree with lighter wood density can be harvested sooner, providing faster income but with lower value per cubic meter (Zhang 2003).

The directly measured traits, following the guidelines of Perez-Harguindeguy et al. (2013), include LA, SLA, SLW, and LDMC. Musaceae's SSD was also measured using a simplified methodology adapted from Perez-Harguindeguy et al. (2013) to confirm and corroborate bibliographic data. Hmax, SSD, LNC, LPC, and N:P were obtained from the bibliography by consulting specific databases for functional traits and scientific publications (Henry et al. 2013; Orwa et al. 2009; de Sousa 2017; de Sousa et al. 2019; Kattge et al. 2020).

Trait values from bibliographic sources were deemed suitable for inclusion in this research when they met multiple integrity criteria. The potential data underwent filtration based on criteria such as being described at the species level, published as a scientific paper, or, secondarily, being an approved academic thesis. Additionally, preference was given to data that originated as closely as possible to the study site and corresponded to the same climate zone of humid tropics. The quality of the data underwent thorough scrutiny, involving the reading of filtered publications and assessing if they closely adhered to the protocols described by Perez-Harguindeguy et al. (2013). In cases where no publications met these criteria, flexibility was introduced, initially by accepting data from slightly more distant locations while still retaining the same climate zone, and subsequently by expanding to other climate zones, utilizing traits at the genus level. As a last resort, data from unpublished papers available in online trait databases were included. Most of the chosen traits adhered to the initially mentioned quality criteria.

To measure LA, SLA, SLW, and LDMC, we collected five sun-exposed leaves (or as much exposed to the sun as possible for cacao leaves) from two different branches of five mature trees, resulting in a total of 25 leaves. These samples were gathered from various locations in the study region, covering the 30,000m<sup>2</sup> of the studied plots and additional sites where the studied species were observed. The distance between sampled trees of the same species ranged from 20m to approximately 100km. The leaves were collected using a telescopic tree pruner and climbing when necessary (Perez-Harguindeguy et al. 2013).

The leaves were immediately placed inside a plastic bag and stored in a container with ice. Subsequently, they were kept in cold storage and analyzed after a few hours, or up to a maximum of 3 days. Prior to measurement, the branches were rehydrated for 30 minutes to a few hours, ensuring the measurement of water-saturated leaves.

The first measurement was the leaf fresh mass (LFM), without petiole, performed with a precision balance with a two-decimal scale. Then, leaf area (LA) was measured with a table scanner. Following this, the leaves were dried for at least 72 hours in an oven at 70°C, and after taking the samples from the oven, they were immediately weighed on the two-decimal scale balance. The LA was calculated using the ImageJ software, with the LeafArea package (run.ij function) in R software. The measurements of LA, LFM, and leaf dry weight were used to calculate SLA, SLW, and LDMC.

The Musaceae specific-stem density (SSD) was determined by taking two similar size pieces from two sections of the pseudo-stem meristem, at 30cm and at 180cm, from 3 Cavendish banana plants located in the same plot, more than 20m apart from each other. The plants were producing fruit when collected. The volume of these banana meristem pieces was measured fresh using a Becker glass

with water and a two-decimal balance to calculate the weight from water displacement. Subsequently, they were dried at 70 degrees for 72 hours, and their weight was measured with a two-decimal scale balance. The SSD for each banana plant was calculated as the average value from the 4 pieces measured for each plant (adapted from Perez-Harguindeguy et al. 2013).

The plant maximum vegetative height ( $H_{max}$ ) for Musaceae was measured using a graduated rod and calculated from the average height of the five taller stems identified in the agroforestry inventory (Perez-Harguindeguy et al. 2013).

*Table 1: Functional traits analyzed and its effect and response functions.*

Functional trait	Unit	Effect function	Response Function	Reference
Plant Maximum Potential Height ( $H_{max}$ )	m	Primary production and biogeochemical processes	Potential longevity, competitive capacity, tolerance to climatic and nutrient stress	(Salgado-Negret 2016, Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013)
Specific Leaf Area (SLA)	$mm^2 \cdot mg^{-1}$	Photosynthetic potential, potential relative growth rate, nitrogen concentration, and others	Leaf defenses, leaf lifespan, carbon fixation rate in leaves, reaction to shade	(Salgado-Negret 2016, Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013)
Specific Leaf Weight (SLW)	$mg \cdot mm^{-2}$	Photosynthetic potential, potential relative growth rate, nitrogen concentration, and others	Leaf defenses, leaf lifespan, carbon fixation rate in leaves, reaction to shade	(Salgado-Negret 2016, Cornelissen et al. 2003, Perez-Harguindeguy et al. 2013)
Leaf Area	$mm^2$	Carbon capture and accumulation, nutrient recycling, biogeochemical processes	Leaf defense, competitive capacity	(Casanoves et al. 2011)
Leaf Nitrogen Concentration (LNC)	$mg \cdot g^{-1}$	Decomposition, biogeochemical processes, photosynthetic rate, growth	Nutrient availability, growth rate	(Salgado-Negret 2016, Perez-Harguindeguy et al. 2013)
Leaf Phosphorus Concentration (LPC)	$mg \cdot g^{-1}$	Decomposition, biogeochemical processes, growth	Nutrient availability	(Salgado-Negret 2016, Perez-Harguindeguy et al. 2013)
LNC:LPC ratio (N:P)	-	Decomposition, biogeochemical processes, growth	Growth limitation by nitrogen or phosphorus	(Perez-Harguindeguy et al. 2013, Güsewell y

				Verhoeven 2006, Wright et al. 2004)
Leaf dry-matter content (LDMC)	mg.g <sup>-1</sup>	Decomposition, biogeochemical processes	Leaf defenses, carbon fixation rate in leaves, leaf lifespan	(Salgado-Negret 2016, Perez-Harguindeguy et al. 2013)
Specific stem density (SSD)	g.cm <sup>-3</sup>	Primary production, biogeochemical processes, litter decomposition	Tolerance to natural enemies and drought	(Salgado-Negret 2016)

## 2.4.2 Quantification of functional indices

The functional diversity of the AFS plots was quantified through single trait indices and multi-trait indices, reflecting different aspects of the ecosystem's functional diversity, including the average trait values in a community and the variability of the trait values in a community, respectively. The single trait index analyzed in this research was the Community Weighted Mean (CWM), and the multi-trait indices analyzed were the functional dispersion (FDis) and the quadratic Rao (RaoQ).

The quantification of the functional indices in AFSs depends on two datasets: an agroforestry inventory, encompassing the composition (species identity) and structure (abundance, basal area, aboveground biomass) of a community, and the trait values of the species present in the community.

The composition and structure are utilized to generate a weighting measure, which in this study was the relative basal area, serving as a surrogate for biomass. We considered the relative basal area to be the most appropriate weighting measure for a cocoa AFS. This choice was made because the commonly used weighting measure, relative abundance, could potentially overestimate the impact of species from the lower strata, which are planted in higher densities (primarily cocoa in this case). Simultaneously, it might underestimate the impact of species with relatively low abundance but high biomass, such as the upper strata shade trees.

The species comprising the majority of the basal area, defined as 80% of the total basal area of each plot in this study, are considered dominant species. These dominant species exert a significant influence on ecosystem properties through their functional traits (Grime, 1998). The relative basal area of the dominant species and the trait values associated with these dominants are fundamental datasets used to calculate the functional indices.

The Community Weighted Mean (CWM) is calculated per plot for each trait using Equation 1, where the trait value of each dominant species in the plot is multiplied by its relative basal area. The CWM reveals the dominant functional trait values in the communities and aids in elucidating the mechanisms that drive ecosystem services (Díaz et al. 2007; Finegan et al. 2015; Garnier et al. 2004; Violle et al. 2007).

$$(1) \text{CWM} = \sum_{i=1}^S \text{RBA}_i X_i$$

Where S is the total number of species,  $\text{RBA}_i$  is the Relative Basal Area of the population (BA of the species population divided by the total BA of the dominant species in the community) from the  $i$ -th species and  $X_i$  is the trait value of the  $i$ -th species.



The multi-trait functional indices contribute to understanding the relationships between the plant community and ecosystem properties. This is because the variability of functional traits within a community is linked to the quantity and distribution of ecological strategies present, utilizing multiple resources and influencing ecosystem properties in diverse ways. This phenomenon is known as the niche complementarity hypothesis (Díaz et al. 2011).

The selected multi-trait indices, FDis and Rao's Q, can be computed for simple communities, which is a requirement for comparing the simple AFSs considered in this study, involving less than three species. Both indices measure trait dispersion, reflecting the differentiation of ecological strategies and the range of niches explored within the community. The distinction between the two lies in their calculations: Rao's Q assesses the mean distance between all possible pairs of species in the community, weighted by their relative abundances, while FDis measures the mean distance of individual species to the centroid of all species in the community (Laliberté and Legendre 2010). In essence, Rao's Q is influenced by species richness or the quantity of significantly different traits, and FDis is not affected by the addition of new traits. The average distance between the traits remains unaffected in FDis (Laliberté and Legendre 2010).

The CWM and the multi-trait indices were calculated using the FD package in R (dataFD function).

## 2.5 Quantification of ecosystem services

Three types of ecosystem services were analyzed: a provisioning service, a regulation service, and a support service.

The measured provisioning service was cocoa productivity, expressed in kilograms of dry cocoa per hectare per year. This assessment was conducted through semi-structured interviews (annex 1) administered to the property owners. Two complementary AFS provisioning proxies were quantified through the agroforestry inventory: timber and fruit tree species richness, and timber trees, fruit trees, and Musaceae plant densities (measured in trees per hectare). These measures were considered representations of AFS provision, as exploitable species richness and densities have the potential to impact income diversification and gross income, in addition to their potential contribution to household consumption.

The climate regulation service considered was the aboveground carbon stored in trees, encompassing all shade trees, Musaceae, and cocoa. The aboveground carbon (Mg/ha) was determined based on field measurements of the diameter at breast height (DBH) using a diametric tape and the total plant height using an analog clinometer for tall trees and a calibrated rod for cocoa and Musaceae. The DBH and total height were applied in preexisting allometric equations (see Table 10 in the annex session), incorporating wood density from databases (Zanne 2009, Kattge et al. 2020) depending on the equation. The resulting aboveground biomass was converted into carbon stock by multiplying it by the carbon fraction of 0.47 (IPCC 2006).

The support service analyzed was soil fertility, measured through soil analysis from the 5 to 20 cm layer. To evaluate soil fertility, we analyzed nitrogen (N), phosphorus (P), potassium (K), acidity, soil organic carbon (C), and also developed a composite soil fertility index to represent the overall fertility condition.

The composite soil fertility index (Fertindex) is graded as a "the more, the better" index. It was calculated by: 1) converting acidity to its inverse value with  $\text{Inverse Acidity} = 1 - \text{Acidity}$ ; 2) standardizing N, P, K, and inverse acidity from 0 to 1; 3) adding all the variables. This Fertindex was deemed satisfactory as it showed a significant relationship with cocoa productivity ( $p\text{-value} = 0.0443$ ;  $\alpha=0.05$ ) in a linear regression (Figure 3). The index was solely used as a response variable, not as a regressor.

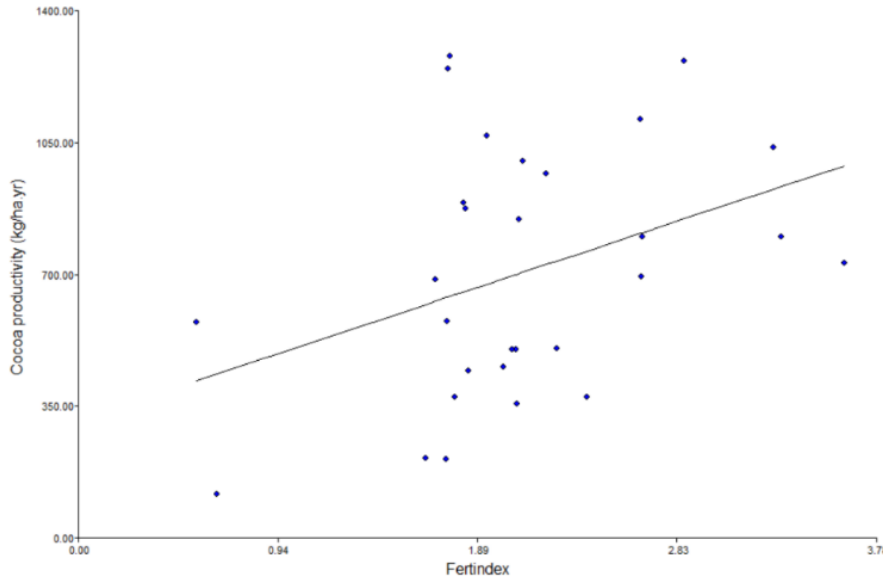


Figure 4: Validation of the Fertindex with a linear regression analysis with the cocoa productivity.

To simultaneously assess multiple environmental services, the three ecosystem services groups—carbon storage, provisioning, and soil fertility—were combined into a composite index. This index standardized the measurement units for all variables and aggregated the values of all ecosystem services, following the approach outlined by Kearney et al. (2019).

Two composite indices for total ecosystem services were generated. The first one, termed the simple ecosystem service index, considered total aboveground carbon, soil fertility (including N, P, K, acidity), and cocoa productivity. The second one, called the complete ecosystem service index, incorporated the same variables but merged cocoa productivity with the densities of timber, fruit trees, and Musaceae into a single provisioning variable. This second index reflects potential provision, as it doesn't measure the quantities of timber and fruit being harvested or the income they generate; instead, it considers all timber and fruit trees (with more than 5cm DBH) measured in the agroforestry inventory as potential sources for provisioning.

To calculate the composite ecosystem service indices, the values of all environmental services indicators were first standardized from 0.1 to 1 (equation 2).

$$(2) Y_i = 0.1 + \frac{(\alpha_i - b_i)}{(a_i - b_i)} \times 0.9$$

Where  $Y$  is the score of the variable  $i$ ,  $\alpha$  is the original value of the variable,  $a$  is the maximum and  $b$  is the minimum observed value of the variable  $i$ .

While Equation 2 for carbon storage and cocoa provisioning directly yields their standardized indices, the ecosystem service categories that include variables with different units, such as soil fertility and potential provisioning, result in scores from a composite index. This index is calculated by standardizing the value of each standardized variable (from Equation ix) and summing up these values after multiplying them by a weighting factor—their respective eigenvectors resulting from a Principal Component Analysis (PCA) with the variables of the ecosystem service category (Equation 3) (Kearney et al. 2019).

$$(3) CI = \sum_{i=1}^n (Y_i W_{i,pc1} + Y_i W_{i,pc2})$$

Where CI is the composite index,  $Y_i$  is the standardized value from the equation 2 of each variable  $i$ , for  $n$  variables and  $W$  are the weighting factors from the first and second axis from the PCA.

Finally, the CI (equation 3) is applied again in the equation 2 to standardize its value in the range between 0.1 and 1 (Kearney et al. 2019), and all the resulting scores from the different ecosystem service categories are added.

## 2.6 Determination of the relationship between functional diversity and the production of ecosystem services

To evaluate the effect of functional diversity on ecosystem services, a series of multiple regressions were performed using a forward selection with “adespatial” package in the R Software (forward.sel function) to select the significant explanatory variables ( $\alpha=0.05$ ), and the multiple regressions were executed using Extended and Mixed Linear Models with Infostat.

The dependent variables included total aboveground carbon, shade tree carbon, soil organic carbon (SOC), cocoa productivity, N, P, K, the composite soil fertility indices, the simple ecosystem service index, and the complete ecosystem service index.

Independent variables across all models included the Community-Weighted Means (CWMs) of SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, and N:P, along with the multi-trait functional indices FDis and RaoQ. The impact of abiotic factors on the response variable was also assessed. For total aboveground carbon and shade tree carbon, the study examined soil parameters: N, P, K, Acidity, and soil texture. In the case of cocoa productivity, the same independent variables were tested, and the shade percentage variable was included. For fertility-related parameters (N, P, K, and the composite soil fertility), as well as for the two ecosystem service composite indices, the considered abiotic factor was solely soil texture (Table 2). The variable selection also included the quadratic term for all independent variables.

All the models considered the random effect of location, a dummy variable representing the Sixaola river basin location, where the plots are susceptible to flood events, and outside of the Sixaola river basin, where flood events do not occur, or at least not as often as in the Sixaola river basin.

Response and explanatory variables were standardized from 0 to 1 to mitigate the scale influence in the selection algorithm. All independent variables were then included in a single model for each response variable, aiming to identify the most significant predictors for its variability.

Utilizing the forward selection method, the independent variables with a significant effect on the response variable were identified. Subsequently, in Infostat, models with the previously selected variables were tested using Extended and Mixed Linear Models. The multiple regression models incorporated location, a dummy variable, as a random effect to account for the influence of being in the river basin or in dry land. To determine the best-fit model, a procedure was followed, involving the inclusion of the previously selected variables in an Extended and Mixed Linear Model. This process considered the correction of normality and homoscedasticity issues using varExp and compared the models based on the Aikaike criteria (AIC). A backward selection was then applied to retain only the variables with a significant p-value ( $\alpha=0.05$ ).

Table 2: Variables included in the multiple regression models.

Ecosystem service	Dependent variable	Independent variable		
		Abiotic	Single trait indices	Multi-trait indices

<b>Carbon stocks</b>	<b>Total aboveground carbon</b>	Location, Soil texture, N, P, K, soil acidity, pH	SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, N:P	FDis, RaoQ
	<b>Shade tree above-ground carbon</b>			
<b>Soil Fertility</b>	<b>Nitrogen</b>	Location, soil texture	SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, N:P	FDis, RaoQ
	<b>Phosphorus</b>			
	<b>Potassium</b>			
	<b>Soil organic carbon</b>			
	<b>Acidity</b>			
<b>Composite soil fertility index</b>				
<b>Provisioning</b>	<b>Cocoa productivity</b>	Location, soil texture, N, P, K, soil acidity, pH, shade	SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, N:P	FDis, RaoQ
<b>Composite ES index</b>	<b>Simple ecosystem service index</b>	Location, soil texture	SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, N:P	FDis, RaoQ
	<b>Complete ecosystem service index</b>	Location, soil texture	SSD, SLA, LDMC, LA, SLW, Hmax, LNC, LPC, N:P	FDis, RaoQ

### 3. Results

The AFS plots ranged from five to fifteen years, with an average of 9.5 years, considered mature cocoa AFSs. The cocoa AFSs were from 0.5ha to 14ha, with an average of 3.5ha.

#### 3.1 Characterization of taxonomic diversity

A total of forty-five tree species, including cacao, were identified in the 30 AFS plots, encompassing a total of 30,000m<sup>2</sup> when considering all the plots, with clonal cocoa in the Huetar Caribbean region of Costa Rica. Among these species, twenty-eight were deemed dominant based on the Mass Ratio Hypothesis (plants forming part of 80% of the shade trees' basal area in each plot, highlighted in bold text) (Table 3).

*Theobroma cacao* was the most dominant species, with the highest basal area per hectare, and is the most common species in all the thirty plots. Among the shade tree species, the most common in cacao AFSs were *Cordia alliodora*, *Musaceae*s (banana and platan), and *Nephelium lappaceum*, present in more than 30% of the plots (frequency>10). Most of the species identified in AFSs were resource trees, with commercial uses for timber or fruit, but there were also seven leguminous tree species used to enhance soil fertility and twelve tree species with non-commercial use or without direct utility were recorded (Table 3).

*Table 3: General statistics of species across all plots, with frequency of species presence, average density of trees per hectare and average basal area (m<sup>2</sup>) of species per hectare. The last column presents the common commercial timber (T), fruit (F) trees, and the leguminous trees (L).*

Specie	Fre- quency	Avg. density/ha	Min. density	Max. density	Avg. BA/ha	Uses
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		$\pm$ S.E.			$\pm$ SE	
<b><i>Theobroma cacao</i></b>	<b>30</b>	<b>756.3 <math>\pm</math> 30.6</b>	<b>470</b>	<b>1060</b>	<b>10.3 <math>\pm</math> 0.6</b>	<b>F</b>
<b><i>Cordia alliodora</i></b>	<b>20</b>	<b>92.5 <math>\pm</math> 28.5</b>	<b>10</b>	<b>610</b>	<b>5.9 <math>\pm</math> 1.4</b>	<b>T</b>
<b><i>Musaceae</i></b>	<b>18</b>	<b>183.3 <math>\pm</math> 48.5</b>	<b>10</b>	<b>620</b>	<b>3.3 <math>\pm</math> 0.8</b>	<b>F</b>
<b><i>Nephelium lappaceum</i></b>	<b>11</b>	<b>35.4 <math>\pm</math> 10.2</b>	<b>10</b>	<b>120</b>	<b>1.3 <math>\pm</math> 0.5</b>	<b>F</b>
<b><i>Bactris gasipaes</i></b>	<b>8</b>	<b>58.7 <math>\pm</math> 20.2</b>	<b>10</b>	<b>190</b>	<b>1.5 <math>\pm</math> 0.6</b>	<b>F</b>
<b><i>Cedrela odorata</i></b>	<b>8</b>	<b>37.5 <math>\pm</math> 16.0</b>	<b>10</b>	<b>140</b>	<b>3.5 <math>\pm</math> 1.8</b>	<b>T</b>
<b><i>Cocos nucifera</i></b>	<b>6</b>	<b>31.7 <math>\pm</math> 12.5</b>	<b>10</b>	<b>90</b>	<b>1.3 <math>\pm</math> 0.5</b>	<b>F</b>
<b><i>Hieronyma alchorroides</i></b>	<b>6</b>	<b>30.0 <math>\pm</math> 7.7</b>	<b>10</b>	<b>50</b>	<b>2.3 <math>\pm</math> 0.7</b>	<b>T</b>
<b><i>Persea americana</i></b>	<b>6</b>	<b>16.7 <math>\pm</math> 3.3</b>	<b>10</b>	<b>30</b>	<b>0.4 <math>\pm</math> 0.1</b>	<b>F</b>
<i>Annona muricata</i>	5	26.0 $\pm$ 9.3	10	60	0.2 $\pm$ 0.1	F
<b><i>Citrus spp</i></b>	<b>5</b>	<b>18.0 <math>\pm</math> 3.7</b>	<b>10</b>	<b>30</b>	<b>0.2 <math>\pm</math> 0.1</b>	<b>F</b>
<b><i>Spondias mombin</i></b>	<b>5</b>	<b>20.0 <math>\pm</math> 4.5</b>	<b>10</b>	<b>30</b>	<b>5.1 <math>\pm</math> 1.4</b>	<b>-</b>
<b><i>Chloroleucon eurycyclum</i></b>	<b>4</b>	<b>12.5 <math>\pm</math> 2.5</b>	<b>10</b>	<b>20</b>	<b>2.6 <math>\pm</math> 0.9</b>	<b>T, L</b>
<b><i>Chrysophyllum cainito</i></b>	<b>4</b>	<b>25.0 <math>\pm</math> 11.9</b>	<b>10</b>	<b>60</b>	<b>0.8 <math>\pm</math> 0.3</b>	<b>F</b>
<i>Dipteryx panamensis</i>	4	12.5 $\pm$ 2.5	10	20	0.6 $\pm$ 0.2	T
<b><i>Erythrina poeppigiana</i></b>	<b>4</b>	<b>12.5 <math>\pm</math> 2.5</b>	<b>10</b>	<b>20</b>	<b>5.8 <math>\pm</math> 1.5</b>	<b>L</b>
<i>Gliricidia sepium</i>	4	20.0 $\pm$ 5.8	10	30	0.3 $\pm$ 0.1	L
<b><i>Luehea seemannii</i></b>	<b>4</b>	<b>17.5 <math>\pm</math> 7.5</b>	<b>0</b>	<b>30</b>	<b>3.5 <math>\pm</math> 1.2</b>	<b>-</b>
<b><i>Inga edulis</i></b>	<b>3</b>	<b>16.7 <math>\pm</math> 6.7</b>	<b>10</b>	<b>30</b>	<b>0.9 <math>\pm</math> 0.5</b>	<b>L</b>
<b><i>Tabebuia rosea</i></b>	<b>3</b>	<b>73.3 <math>\pm</math> 58.4</b>	<b>10</b>	<b>190</b>	<b>4.5 <math>\pm</math> 2.7</b>	<b>T</b>
<b><i>Annona papilionella</i></b>	<b>2</b>	<b>15.0 <math>\pm</math> 5.0</b>	<b>10</b>	<b>20</b>	<b>2.6 <math>\pm</math> 0.5</b>	<b>-</b>
<i>Cecropia sp</i>	2	10.0 $\pm$ 0.0	10	10	0.5 $\pm$ 0.3	-
<b><i>Leucaena leucocephala</i></b>	<b>2</b>	<b>100.0 <math>\pm</math> 70.0</b>	<b>30</b>	<b>170</b>	<b>3.7 <math>\pm</math> 3.0</b>	<b>L</b>
<b><i>Mangifera indica</i></b>	<b>2</b>	<b>20.0 <math>\pm</math> 0.0</b>	<b>20</b>	<b>20</b>	<b>1.7 <math>\pm</math> 0.3</b>	<b>F</b>
<i>Psidium guajava</i>	2	10.0 $\pm$ 0.0	10	10	0.3 $\pm$ 0.2	F
<b><i>Spondias dulcis</i></b>	<b>2</b>	<b>15.0 <math>\pm</math> 5.0</b>	<b>10</b>	<b>20</b>	<b>0.6 <math>\pm</math> 0.5</b>	<b>F</b>
<i>Swietenia Macrophylla</i>	2	15.0 $\pm$ 5.0	10	20	0.4 $\pm$ 0.3	T
<b><i>Terminalia oblonga</i></b>	<b>2</b>	<b>20.0 <math>\pm</math> 10.0</b>	<b>10</b>	<b>30</b>	<b>1.4 <math>\pm</math> 1.1</b>	<b>T</b>
<b><i>Zanthoxylum riedelianum</i></b>	<b>2</b>	<b>20.0 <math>\pm</math> 10.0</b>	<b>10</b>	<b>30</b>	<b>0.9 <math>\pm</math> 0.8</b>	<b>-</b>
<b><i>Anacardium excelsum</i></b>	<b>1</b>	<b>10.0</b>	<b>10</b>	<b>10</b>	<b>0.5 <math>\pm</math> 0.0</b>	<b>T</b>
<i>Annona mucosa</i>	1	10.0	10	10	0.3	F
<i>Artocarpus heterophyllus</i>	1	10.0	10	10	0.1	F
<i>Carica papaya</i>	1	10.0	10	10	0.1	F
<i>Cassia grandis</i>	1	20.0	20	20	0.4	-
<i>Erythrina fusca</i>	1	20.0	20	20	0.3	L
<i>Ficus insipida</i>	1	10.0	10	10	0.7	-
<b><i>Hura crepitans</i></b>	<b>1</b>	<b>10.0</b>	<b>10</b>	<b>10</b>	<b>28.9</b>	<b>-</b>
<i>Psidium friedrichsthalium</i>	1	10.0	10	10	0.1	F
<i>Pterocarpus officinalis</i>	1	10.0	10	10	2.0	-
<b><i>Sapium glandulosum</i></b>	<b>1</b>	<b>30.0</b>	<b>30</b>	<b>30</b>	<b>5.1</b>	<b>-</b>
<b><i>Shizolobium parahyba</i></b>	<b>1</b>	<b>20.0</b>	<b>20</b>	<b>20</b>	<b>4.5</b>	<b>T, L</b>
<i>Simarouba amara</i>	1	10.0	10	10	0.4	-
<b><i>Spondias purpurea</i></b>	<b>1</b>	<b>30.0</b>	<b>30</b>	<b>30</b>	<b>1.7</b>	<b>F</b>
<i>Syzygium malaccense</i>	1	10.0	10	10	0.7	F

<i>Trophis racemosa</i>	1	10.0	10	10	0.2	-
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### 3.2 Characterization of functional traits

Table 4 presents the Spearman correlation between the functional traits for the studied species. Negative correlations were observed between SLA and LDMC, SLW and SSD, while a positive correlation was found between SLA and LNC. Additionally, LDMC showed a positive correlation with SLW and SSD. SLW also exhibited a negative correlation with LNC and a positive correlation with SSD. LNC displayed a positive correlation with LPC and N:P, while LPC had a negative correlation with N:P.

*Table 4: Spearman correlation between functional traits for the studied species. In the top diagonal of the table are the p-values, with significant correlations in bold text. In the lower diagonal are the correlation values.*

	SSD	SLA	LDMC	LA	SLW	Hmax	LNC	LPC	NP
SSD	1.000	<b>0.018</b>	<b>0.013</b>	0.057	<b>0.018</b>	0.433	0.424	0.584	0.502
SLA	<b>-0.456</b>	1.000	<b>0.002</b>	0.468	<b>&lt;0.0001</b>	0.929	<b>0.001</b>	0.492	0.069
LDMC	<b>0.479</b>	<b>-0.585</b>	1.000	0.880	<b>0.002</b>	0.604	0.193	0.676	0.326
LA	-0.366	0.140	-0.029	1.000	0.468	0.994	0.465	0.359	0.697
SLW	<b>0.456</b>	<b>-1.000</b>	<b>0.585</b>	-0.140	1.000	0.929	<b>0.001</b>	0.492	0.069
Hmax	-0.154	-0.018	0.102	-0.001	0.018	1.000	0.593	0.067	0.074
LNC	-0.154	<b>0.645</b>	-0.251	0.141	<b>-0.645</b>	0.106	1.000	<b>0.049</b>	<b>0.017</b>
LPC	-0.108	0.136	0.083	0.180	-0.136	0.351	<b>0.375</b>	1.000	<b>0.002</b>
NP	0.129	0.350	-0.189	-0.075	-0.350	-0.343	<b>0.458</b>	<b>-0.563</b>	1.000

SSD: Stem specific density; SLA: Specific leaf area. LDMC: Leaf dry matter content; LA: Leaf area; SLW: Specific Leaf Area; Hmax: Maximum potential height; LNC: Leaf nitrogen concentration; LPC: Leaf phosphorus concentration; NP: Leaf nitrogen:phosphorus ratio.

Using the functional traits, the species were separated into six Plant Functional Types (PFT). The functional groups were not used for inferential statistical analysis, but they support the description of the species contributions in the AFS dynamics based on their functional profiles.

The PFT were defined by previously separating two groups a priori: the Arecaceae, composed by *Bactris gasipaes* (peach palm) and *Cocos nucifera* (coconut), and the Musaceae, composed by *Musa acuminata* (cavendish banana) and *Musa paradisiaca* (plantain). This is due to their distinct phylogeny from the class of dicotyledon trees, represented in the rest of the PFG.

The remaining species underwent a cluster analysis using the Ward's method, calculated with Euclidean distance, resulting in three Plant Functional Types (PFT). This cluster analysis was based on leaf traits: SLA, SLW, LNC, LPC, N:P, and LDMC. Leaf traits serve as indicators of plant ecological strategies (Wright et al. 2004), making them useful for distinguishing between Plant Functional Types (PFT).

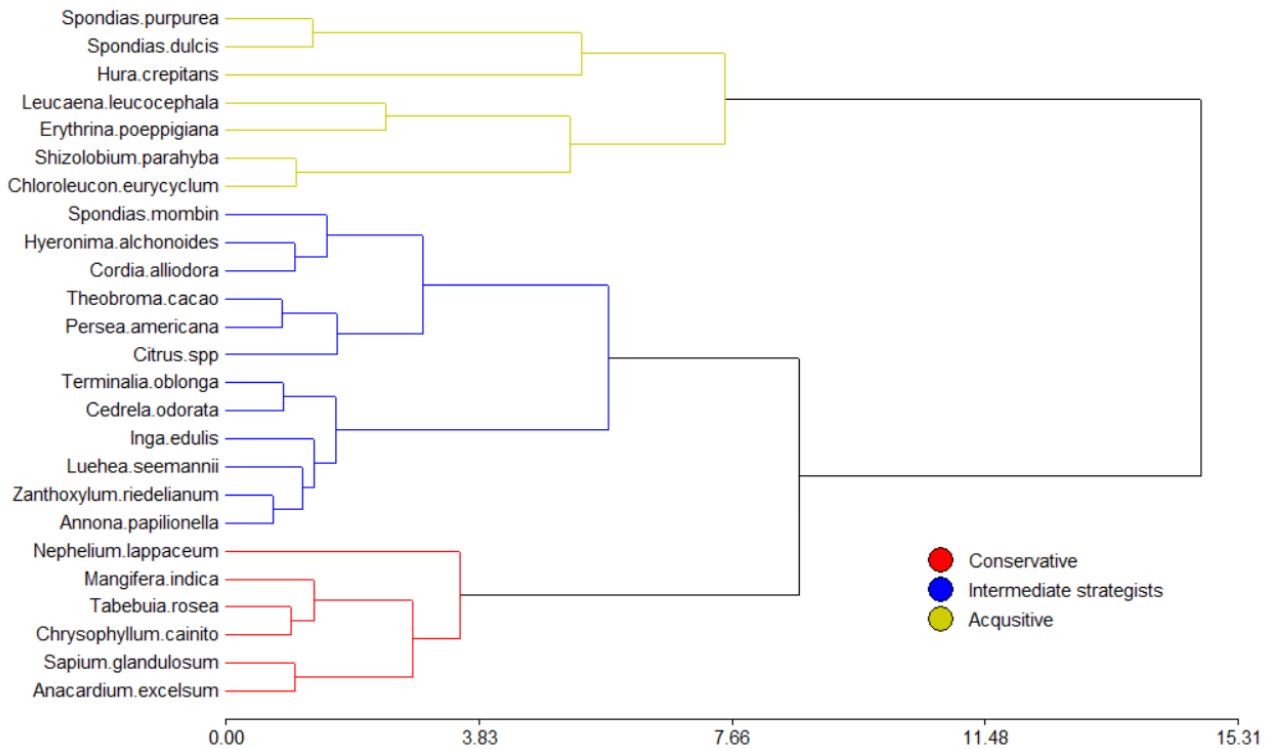


Figure 5: Plant Functional Types (PFT), formed with Cluster analysis using the Ward method and Euclidian distances. The clustering was based on the CWM SLA, SLW, LNC, LPC, N:P and LDMC from the 28 dominant species.

The PFG were satisfied by a MANOVA (Table 5), with significant differences between all the groups ( $p < 0.0001$ ), described by columns with different letters which identify different groups according to the Hotelling test ( $\alpha = 0.05$ ).

Table 5: Multivariate analysis of variance (MANOVA), with Hotteling test ( $\alpha = 0.05$ ), comparing the average values of functional traits between Plant Functional Types.

Cluster	SSD	SLA	LDMC	LA	SLW	Hmax	LNC	LPC	NP					
Musaceae	0.04	14.5	219.8	949731	0.07	5.2	39.5	2.3	17.2	A				
Arecaceae	0.60	7.2	527.6	905852	0.16	25.4	18.7	1.5	13.5		B			
Acquisitive	0.45	18.8	302.6	40053	0.06	24.9	36.1	1.8	23.0			C		
Intermediate strategists	0.53	12.4	404.7	26005	0.08	25.8	23.3	1.3	19.4				D	
Conservative	0.55	8.2	424.9	19632	0.12	26.6	17.7	1.6	12.7					E

Figure 5 is a Principal Component Analysis (PCA) that illustrates the entire plant economic spectrum of the dominant species identified in the cocoa AFS. The distribution of species in this graphic is indicative of their ecological strategy and adaptation to the environment. The first axis accounts for 40.4% of the trait variability and is primarily influenced by SLA, LNC, and N:P ratio on the negative side of the axis, and by LDMC, SLW, LA, and SSD on the positive side. The loadings of the leaf traits play a crucial role in explaining the first axis, aligning with the hypothesis that the leaf economic spectrum aids in assessing plant ecological strategies. The second axis represents 19.6% of the trait variability and is mainly impacted by LPC, Hmax, and LA on the positive side, while the negative side

is influenced by SSD and N:P ratio. The loadings from whole plant traits—Hmax and SSD—are particularly important in describing the second axis, confirming that whole plant traits also contribute significantly to assessing plant ecological strategies (Reich 2014).

The species located on the negative side of the first axis are considered acquisitive and the species on the positive side of the first axis are considered conservative. The species with high SLA, LNC and N:P and with low LDMC, SLW, and SSD are considered the true acquisitive species and are concentrated in left side of the biplot. The leguminous trees are well-represented in this PFT, with only one leguminous species, *Inga edulis*, not being incorporated in it. *Musaceae* share more similar physiological characteristics with this group that with the other group.

On the opposite side of the first axis, towards the far positive end, are the species characterized by high SLW, LDMC, and SSD, denoted as the true conservative species. Table 6 provides additional support, revealing that Hmax is also higher in this group. Although LA exhibits significant variability within the groups, and it is higher in the acquisitive group than in the conservative group, this vector is oriented towards the positive axis due to its relationship with the *Arecaceae* group (Table 6).

The intermediate strategists are more concentrated in the center of the PCA, and are present both in the conservative and the acquisitive side of the leaf economic spectrum, without reaching high values in any of the sides of the first axis. All the traits from this group are intermediate between the conservative and the acquisitive strategists, except to the LPC, that is lower in this groups, due the presence of three fruit species with low LPC: *Theobroma cacao*, *Citrus spp.*, and *Persea americana*.

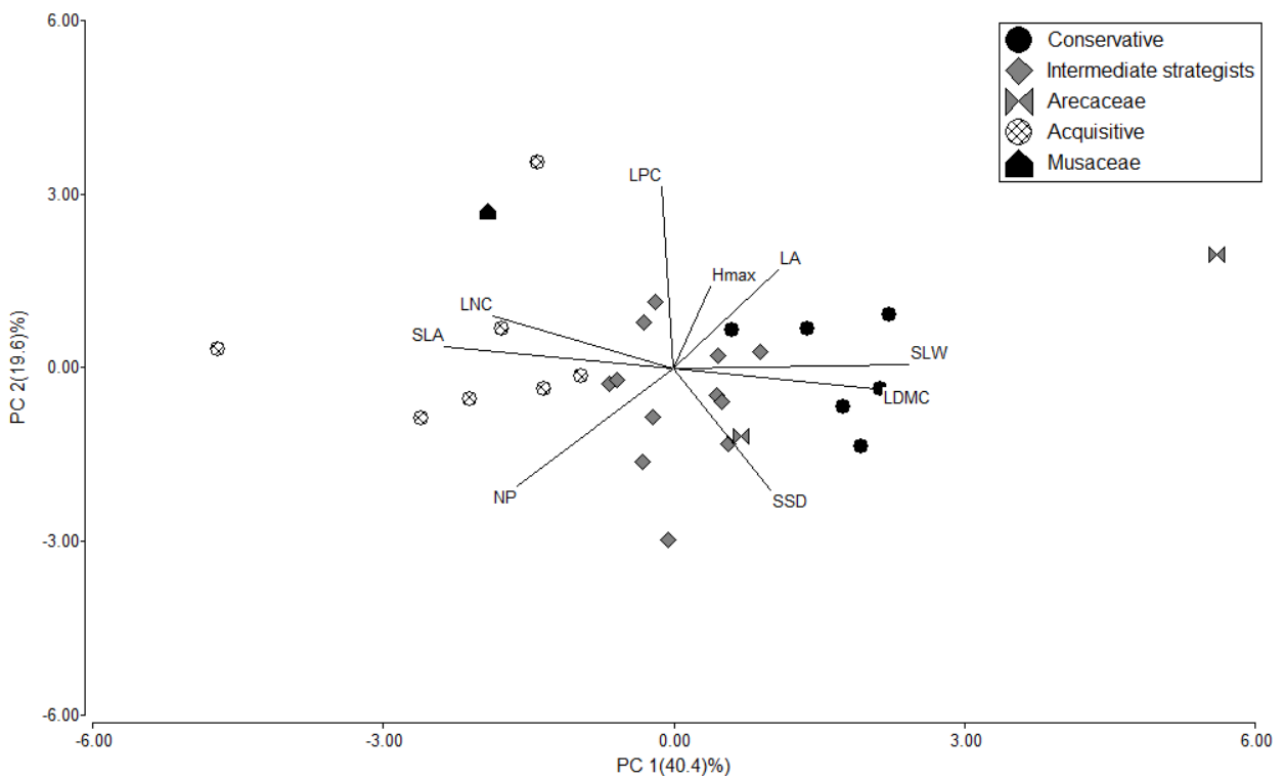


Figure 6: Plant economic spectrum of the dominant AFS species in a Principal Component Analysis. The leaf economic spectrum is represented by the first axis, in which leaf traits hold the greatest loadings. The PFT are identified in the caption.

### 3.3 Definition of AFS groups for ecological complexity characterization



Three AFS groups were defined through the cluster analysis (Figure 6), with significantly different species richness between each other ( $p$ -value $<0.05$ ), setting an appropriate gradient of ecological complexity for the following characterization and comparisons (Table 7 and 8).

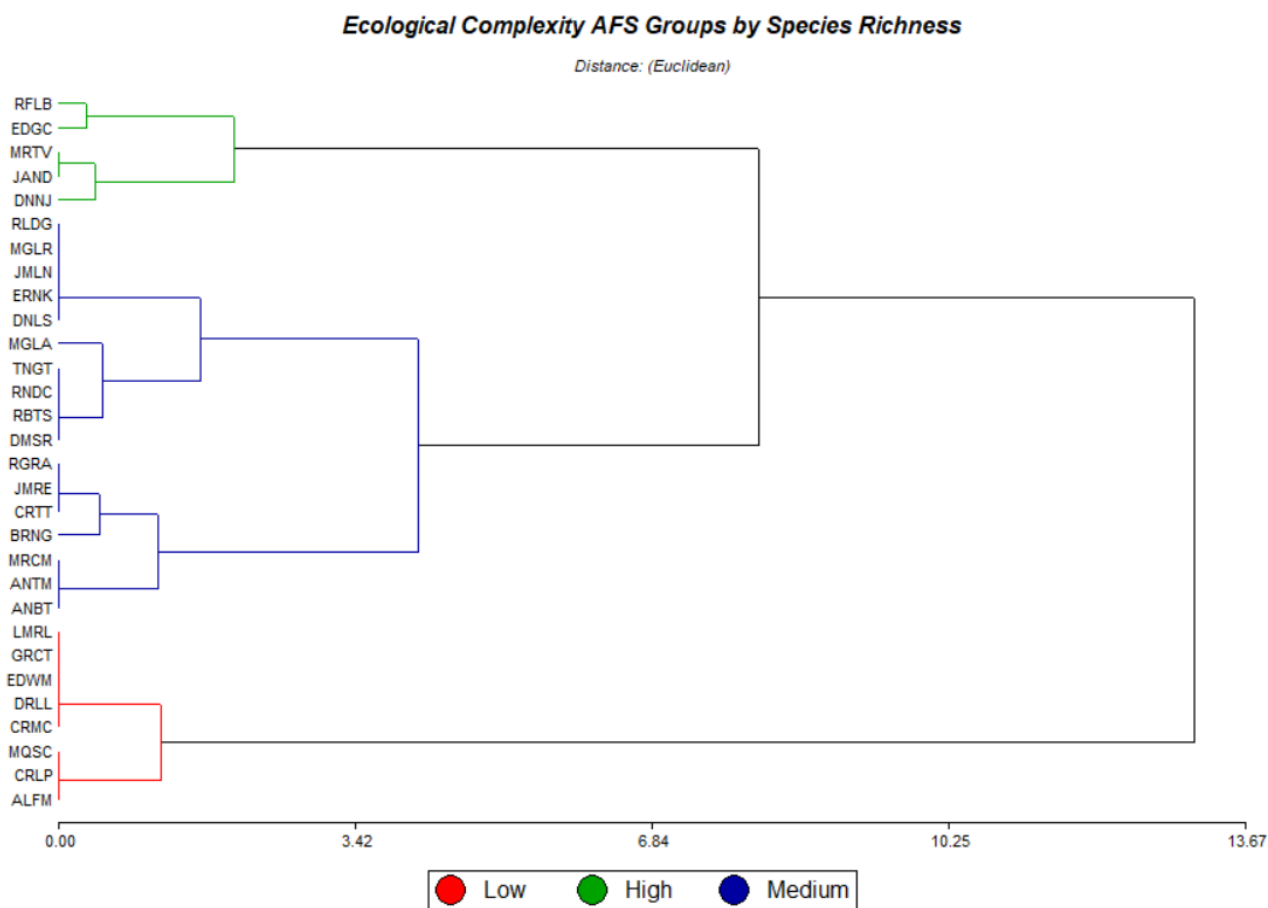


Figure 7: AFS groups based on species richness, classifying plots in three groups with different ecological complexities, the Low complexity group, The Medium complexity group and the High complexity group.

This AFSs not only exhibited variations in species richness but also demonstrated distinct species compositions (Table 6). Aside from *Theobroma cacao*, which was the most prevalent species in all AFS groups, Musaceae was consistently abundant across all AFSs. Among the less common species, there were trees of significant value for conservation, such as *Dipteryx panamensis*, which is protected in Costa Rica due to its importance for macaw preservation (MINAE 1996).

Table 6: List of the five most common and the five rarest species in each AFS group according to their relative abundance (plants/plot), without considering *Theobroma cacao*.

AFS groups	Most common species	Average Relative Abundance	Rarest species	Average Relative Abundance
Low	<i>Tabebuia rosea</i>	0.20	<i>Musa spp</i>	0.05
	<i>Leucaena leucocephala</i>	0.19	<i>Cordia alliodora</i>	0.05
	<i>Nephelium lappaceum</i>	0.11	<i>Hyeronima alchonoides</i>	0.05
	<i>Cocos nucifera</i>	0.10	<i>Cedrela odorata</i>	0.04
	<i>Musa spp</i>	0.05	<i>Bactris gasipaes</i>	0.04
Medium	<i>Musa spp</i>	0.14	<i>Simarouba amara</i>	0.01
	<i>Cordia alliodora</i>	0.09	<i>Psidium guajava</i>	0.01
	<i>Bactris gasipaes</i>	0.07	<i>Artocarpus heterophyllus</i>	0.01
	<i>Hyeronima alchonoides</i>	0.05	<i>Syzygium malaccense</i>	0.01
	<i>Cedrela odorata</i>	0.04	<i>Hura crepitans</i>	0.01
High	<i>Musa spp</i>	0.17	<i>Chloroleucon eurycyclum</i>	0.01
	<i>Cordia alliodora</i>	0.07	<i>Erythrina poeppigiana</i>	0.01
	<i>Annona muricata</i>	0.03	<i>Dipteryx panamensis</i>	0.01
	<i>Cocos nucifera</i>	0.03	<i>Trophis racemosa</i>	0.01
	<i>Bactris gasipaes</i>	0.03	<i>Cecropia sp</i>	0.01

Regarding the overall structure of the tree groups, cocoa tree densities exhibited a marginal difference ( $p$ -value > 0.05) with slightly higher density, though not significantly different, in the Medium complexity group (Table 7). Shade tree density followed the same pattern of our complexity gradient, with a lower value in the Low complexity group, progressively increasing to higher values in the Medium and High complexity groups. The total tree density (including all the trees in the AFS), total basal area, and shade tree basal area were significantly lower in the Low complexity group than in the Medium and High complexity groups. Additionally, the shade percentage was significantly lower in the Low complexity group than in the other two groups.

The shade percentage and elements of the AFS structure, with the exception of cocoa tree density, followed the same pattern of the ecological complexity gradient as described by species richness, increasing from the low complexity group to the high complexity groups. This corroborates the existence of a gradient of ecological complexity across the AFS groups.

### 3.4 Functional diversity characterization

The characterization of functional diversity in the AFS groups focused on analyzing differences in the Community-Weighted Mean (CWM) and multi-trait index among the agroforestry groups (Table 7). The CWM of LNC, SSD, and LDMC were significantly different between the AFS groups ( $p$ -value < 0.05), with inferior values for the Low ecological complexity group compared to the medium and high complexity groups. The low complexity group presented a trait profile associated with the stronger influence of slow-growth and slow-decomposition conservative plant traits, with low LNC and high SSD and LDMC (Garnier et al. 2004, Finegan et al. 2015). The Medium and High complexity groups had a stronger influence of fast-growing and fast decomposition acquisitive plant traits, with higher LNC and low SSD and LDMC (Garnier et al. 2004, Finegan et al. 2015). CWM Hmax presented significant differences between the groups in the ANOVA test; however, the Fisher's LSD posthoc test didn't find significant differences among the groups, which might be related to a reduced power of the analysis due to an insufficient sample size and high variability within the groups. CWM LPC, SLA, SLW, LA did not present significant differences between the groups.

The multi-trait indices FDis and RaoQ did not show a significant difference among the groups. It was expected that higher ecological complexity would lead to a wider range of traits, resulting in higher FDis and RaoQ. However, the wide variability of these indices within these AFS groups did not confirm such a pattern.

Table 7: Comparison across ecological complexity AFS groups. For AFS components densities, Generalized Linear model and LSD Fisher comparison ( $\alpha=0.05$ ) were used. For general AFS characteristics and functional diversity indices, Extended and Mixed Linear Models Analysis ( $\alpha=0.05$  were used). Standard error is presented.  $n=30$ . Different letters in a row indicate significant differences.

Index	Chi-sqr	F-value	p-value	Low	Medium	High
<b>Species richness (n° trees)</b>	<b>40.115</b>	-	<b>&lt;0.0001</b>	<b>2.63 ± 0.57 C</b>	<b>6.65 ± 0.63 B</b>	<b>11.60 ± 1.52 A</b>
Cocoa density (plant/ha)	5.8344	-	0.05409	687.50 ± 49.46 A	814.71 ± 40.10 A	668.00 ± 60.82 A
<b>Shade tree density (plant/ha)</b>	<b>1543</b>	-	<b>&lt;0.0001</b>	<b>117.50 ± 3.83 C</b>	<b>302.94 ± 4.22 B</b>	<b>472.00 ± 9.72 A</b>
<b>Total tree density (plant/ha)</b>	<b>603.68</b>	-	<b>&lt;0.0001</b>	<b>805.00 ± 10.03 B</b>	<b>1117.65 ± 8.11 A</b>	<b>1140.00 ± 15.10 A</b>
<b>*Total basal area (m<sup>2</sup>/ha)</b>	-	<b>6.35</b>	<b>0.0055</b>	<b>17.89 ± 0.78 B</b>	<b>25.70 ± 2.68 A</b>	<b>31.23 ± 5.72 A</b>
<b>*Shade tree basal area (m<sup>2</sup>/ha)</b>	-	<b>6.6</b>	<b>0.0046</b>	<b>6.02 ± 0.96 B</b>	<b>15.59 ± 3.11 A</b>	<b>22.69 ± 7.38 A</b>
<b>Shade (%)</b>	-	<b>3.51</b>	<b>0.0441</b>	<b>30.53 ± 5.01 B</b>	<b>43.30 ± 3.43 A</b>	<b>50.40 ± 6.33 A</b>
Functional indices						
<b>CWM Hmax</b>	-	<b>3.46</b>	<b>0.0459</b>	<b>14.12 ± 0.96 A</b>	<b>18.01 ± 1.40 A</b>	<b>19.59 ± 3.19 A</b>
<b>**CWM LPC</b>	-	2.93	0.0707	1.06 ± 0.09 A	1.25 ± 0.09 A	1.33 ± 0.11 A
<b>**CWM SLA</b>	-	2.39	0.1109	12.05 ± 0.67 A	13.32 ± 0.43 A	13.08 ± 0.7 A
<b>***CWM LNC</b>	-	<b>3.79</b>	<b>0.0355</b>	<b>20.64 ± 1.23 B</b>	<b>25.97 ± 1.38 A</b>	<b>26.17 ± 2.27 A</b>
CWM N:P	-	0.63	0.5392	22.20 ± 0.88 A	22.65 ± 0.60 A	21.24 ± 1.11 A
<b>*CWM SSD</b>	-	<b>7.45</b>	<b>0.0027</b>	<b>0.48 ± 0.01 A</b>	<b>0.43 ± 0.01 B</b>	<b>0.41 ± 0.02 B</b>
<b>***CWM LA</b>	-	2.56	0.096	78721 ± 49502 A	119146 ± 20600 A	165751 ± 59262 A
<b>CWM LDMC</b>	-	<b>3.53</b>	<b>0.0436</b>	<b>415.48 ± 12.37 A</b>	<b>377.37 ± 8.48 B</b>	<b>376.33 ± 15.64 B</b>
<b>*CWM SLW</b>	-	1.7	0.2017	0.089 ± 0.005 A	0.079 ± 0.002 A	0.080 ± 0.004 A
FDis	-	0.78	0.4675	1.74 ± 0.23 A	2.04 ± 0.16 A	2.14 ± 0.29 A
RaoQ	-	1.8	0.4667	4.22 ± 1.01 A	5.54 ± 0.70 A	6.03 ± 1.28 A

\*Variable adjusted by the varident function.

\*\* Variables transformed to a rank, from 1 to 30.

\*\*\*Variables transformed by natural logarithm (ln).

### 3.5 Characterization of ecosystem services of provision in cocoa agroforestry systems along a gradient of ecological complexity

#### 3.5.1 Provisioning in AFSs along a gradient of ecological complexity

The cocoa yield was significantly different among the AFS groups ( $p$ -value  $< 0.05$ ) (Table 8). The low complexity group had the highest cocoa yield, and the medium and high complexity groups produced relatively less. The high complexity group presented the lowest average yield, but also had the biggest variability. When analyzing the cocoa yield per tree, we found no significant differences between the AFS groups (Figure 8 and Table 8).

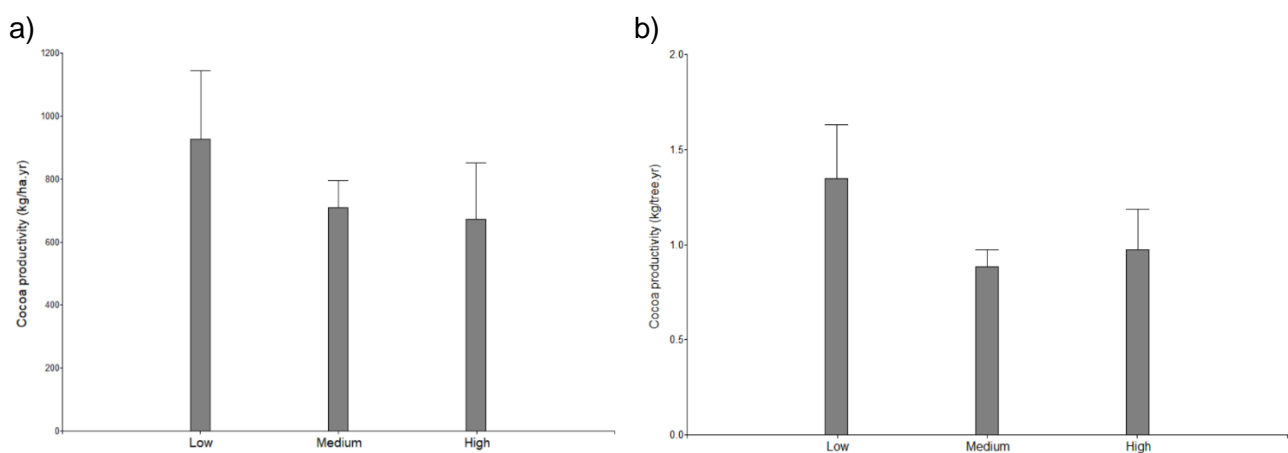


Figure 8: Average cacao yield in AFS groups with different levels of ecological complexity, described a) per hectare, and b) per tree.

Two complementary AFS products were analyzed: timber and fruit trees. Fruit tree species richness and density, as well as the density of timber trees, were considered, as they can potentially impact income diversification and, at least, gross income, respectively. Fruit species richness and fruit tree densities were consistently higher in the Medium and High complexity groups. Timber trees, in contrast, didn't show significant differences across the groups (Figure 8).

*Musaceae*, including banana and plantain, are also very important AFS components for household consumption and for income generation. Besides the clear average difference between the AFS groups, no significant difference was detected due its high variability within the groups. Many systems, independently from which ecological complexity group, did not have *Musaceae*. Nevertheless, is noticeable that AFS plots from the low complexity group had very small densities of *Musaceae* or did not have it at all.

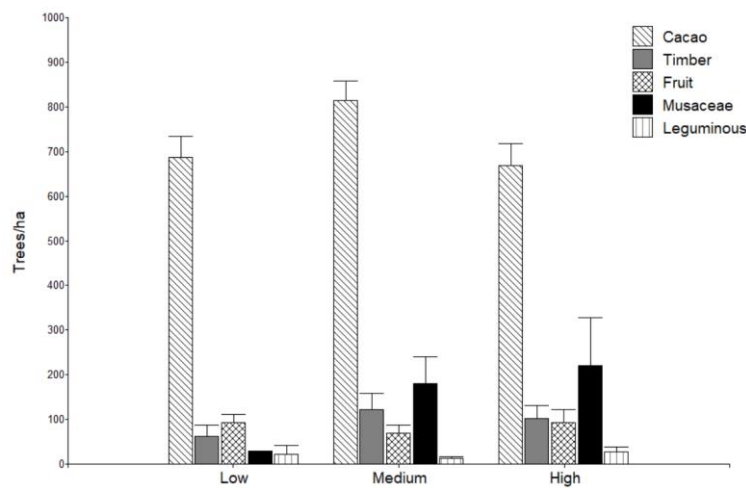


Figure 9: Average tree densities (number of trees per hectare) of cacao, Musaceae, timber, and fruits in AFS groups with different levels of ecological complexity.

### 3.5.2 Aboveground carbon in AFSs along a gradient of ecological complexity

The AFS groups presented significant differences for the aboveground carbon stocks of shade trees and for the total AFS carbon stock (Table 8). The Low complexity group exhibited smaller carbon stocks, with an average of 26.59Mg of carbon per hectare in total. In contrast, the medium and high complexity groups displayed statistically equal carbon stocks, averaging 51.11 and 64.38Mg of carbon per hectare, respectively.

The most significant contribution to the carbon stocks in all the AFS groups were the shade trees, representing in average 75% of the carbon stocks.

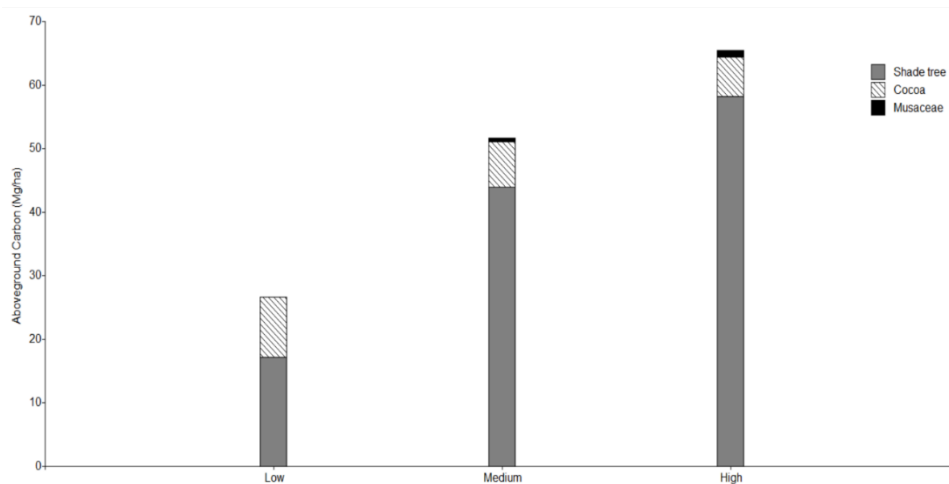


Figure 10: Average aboveground (megagrams of carbon per hectare) from three AFS components, cacao, shade trees, and Musaceae, in tree AFS groups with different levels of ecological complexity.

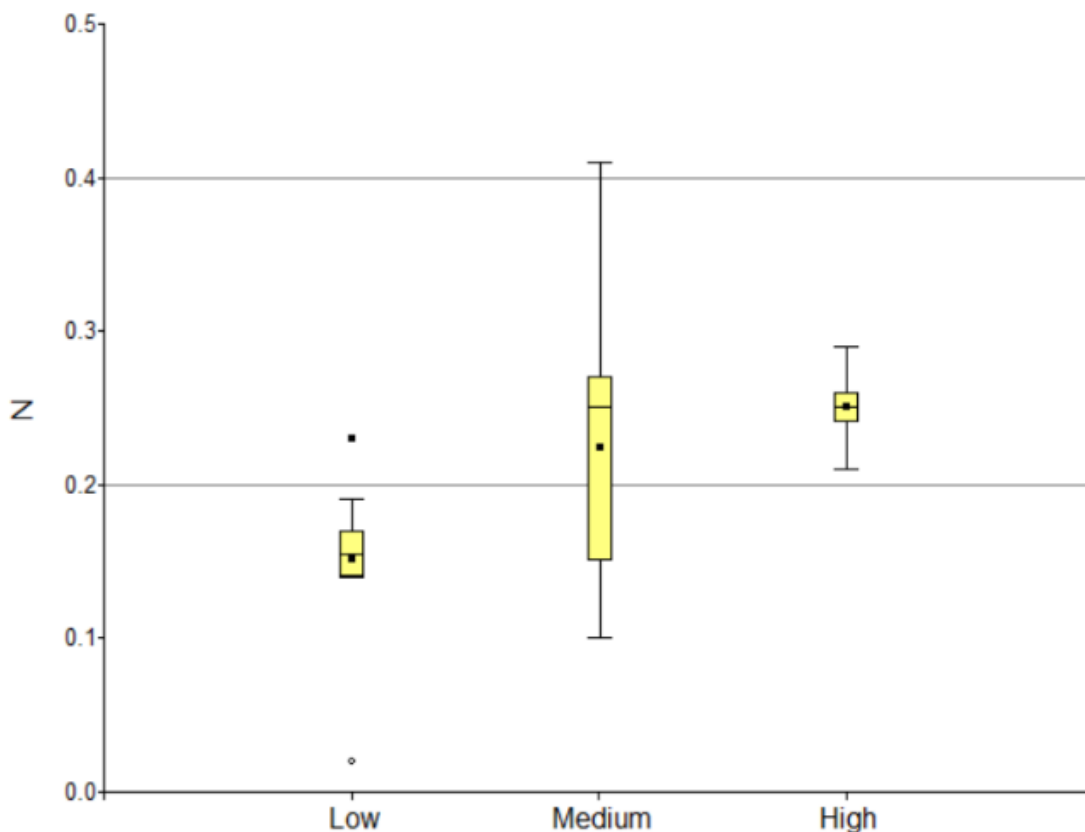
### 3.5.3 Soil fertility in AFSs along a gradient of ecological complexity

Figure 9 presents a descriptive graphic of the chemical soil conditions of the studied cocoa AFSs, with average soil macronutrients and pH thresholds for cacao illustrated in gray horizontal lines, according to (Snoeck et al. 2016).

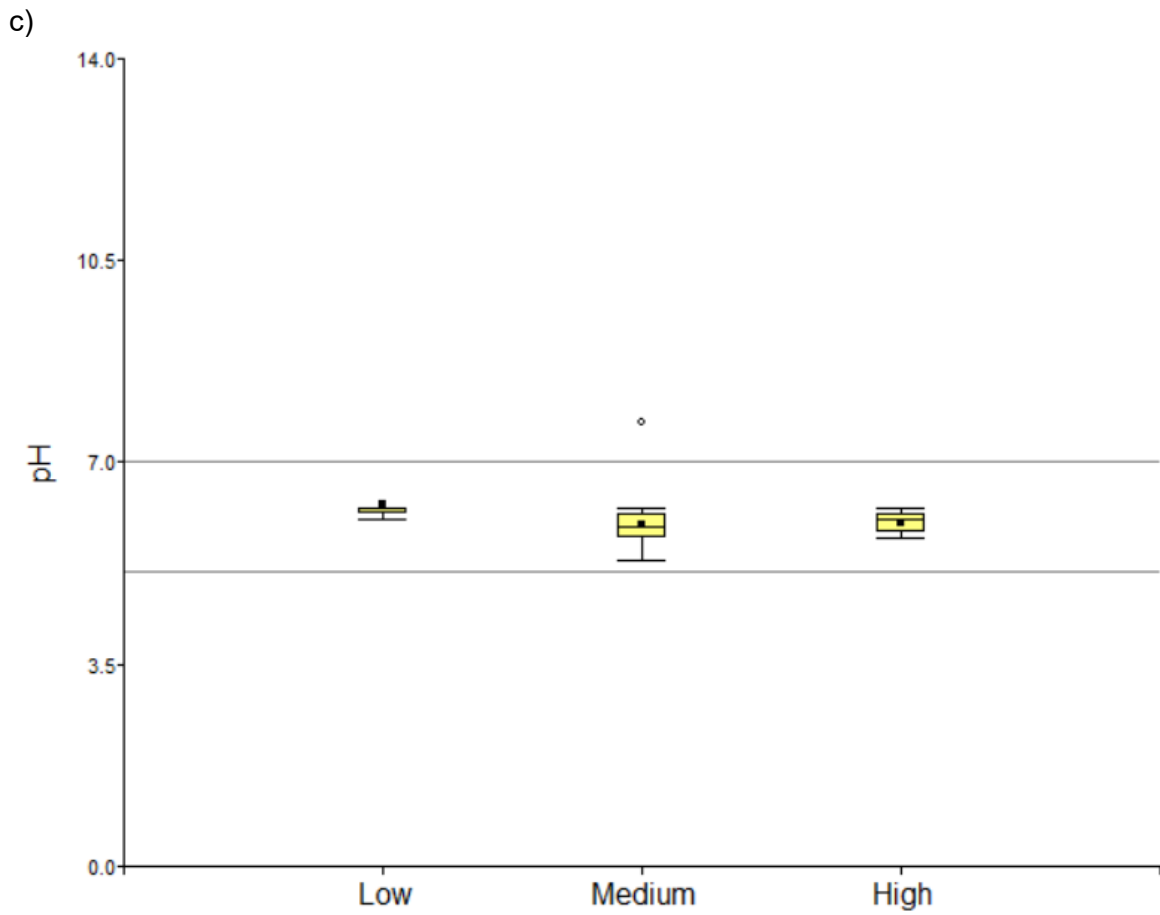
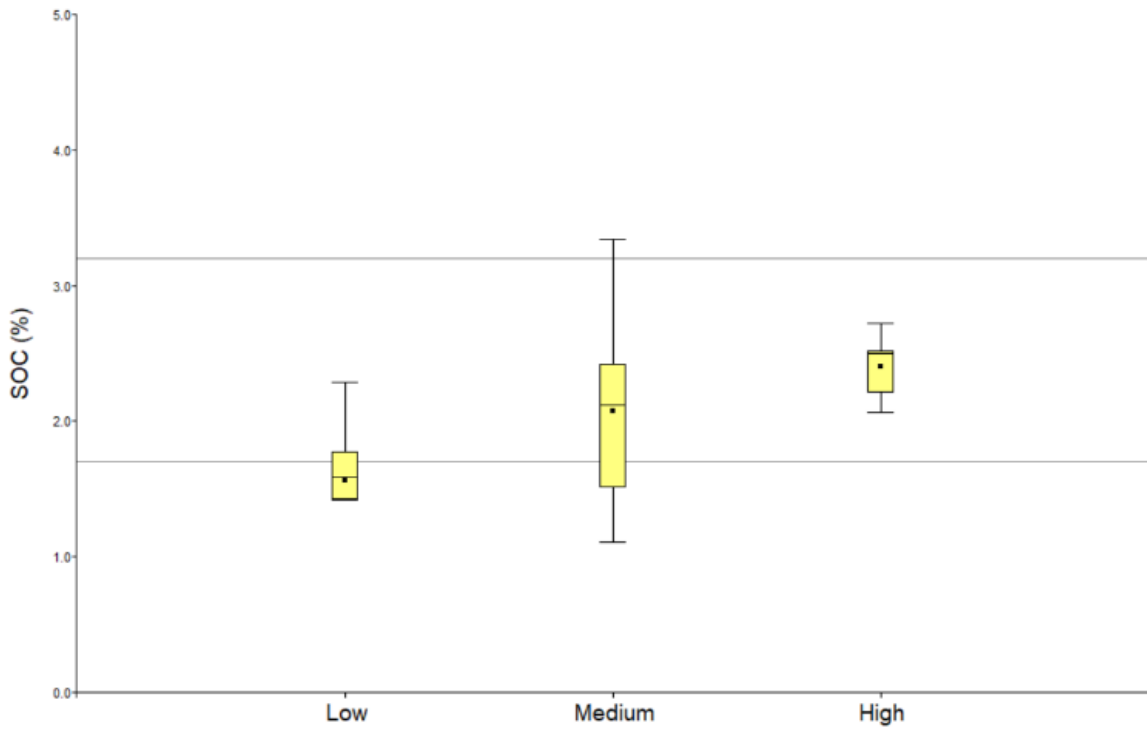
The soil fertility parameters that showed significant differences were nitrogen (N) and soil organic carbon (SOC). The total soil N was significantly lower in the Low complexity group than in the Medium and High complexity groups (Table 8). In the Low complexity group, the levels of N are below the minimum nutrient requirements for cacao, while, on average, the other two groups have adequate levels for this nutrient. SOC was lower in the Low complexity group compared to the High complexity group, and due to high variability, the Medium complexity group couldn't be differentiated from the other AFS groups. On average, the low complexity group falls below the minimum requirements of N and SOC for cacao production.

The pH of all the AFS groups was in the appropriate range for cacao. Phosphorus is deficient in most of the AFS plots. Phosphorus deficiency is expected in highly weathered tropical soils and can affect the AFS's productivity, especially for shade trees, as it is the most important nutrient limitation for tropical tree growth (Grubb 1977). Potassium didn't show significant differences between the AFS groups, and on average, these AFS plots meet the minimum K requirement for cacao production. The composite fertility, representing overall soil fertility, does not differ significantly between the groups.

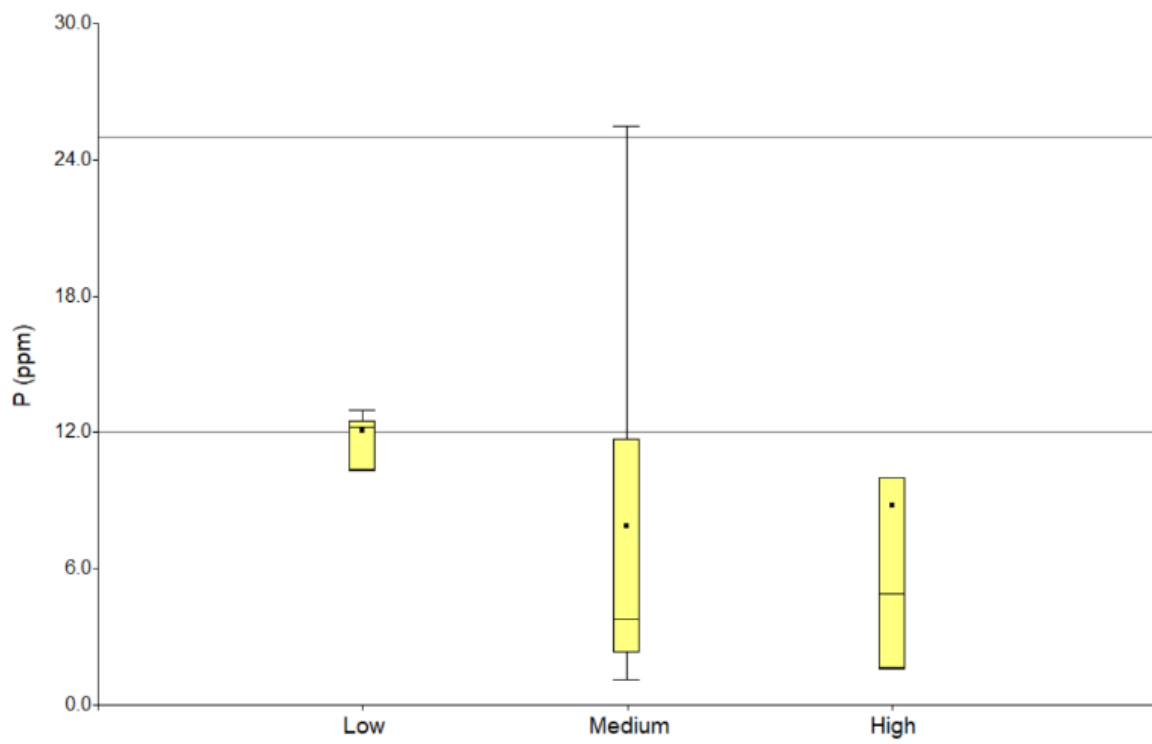
a)



b)







e)

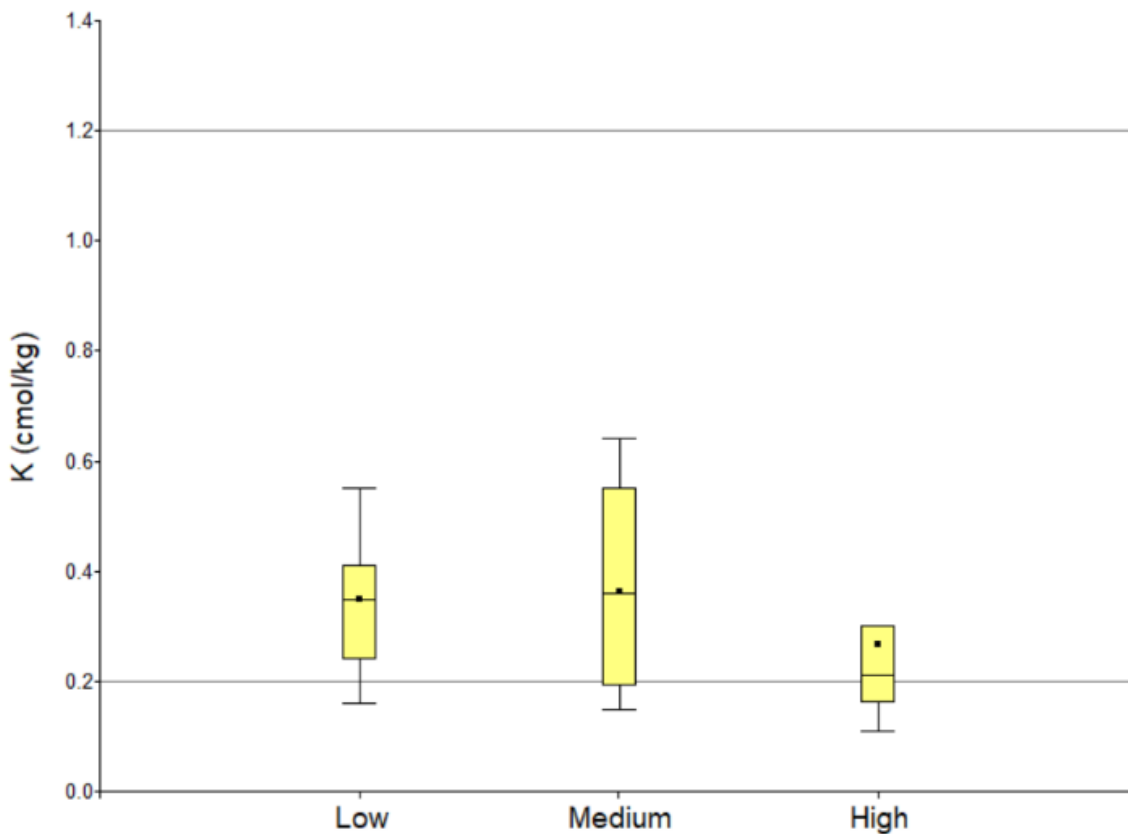


Figure 11: Soil parameters in AFS groups with different levels of ecological complexity. Superior and inferior nutrients and pH thresholds for cocoa are presented in horizontal lines according to Snoeck et al. (2016). a) is the total soil nitrogen (%), b) soil organic carbon (%), c) pH, d) phosphorus (ppm), e) potassium (cmol/kg).

### 3.5.4 Composite ecosystem service index

The simple ecosystem service index, which considers carbon sequestration, soil fertility, and cocoa provision simultaneously, did not show significant differences between the groups (Table 8). The complete ecosystem service index, which adds potential production of fruits, timber, and banana to the provisioning service, exhibited a significant difference across the AFS groups. The Low AFS group had an inferior value compared to the Medium and High complexity AFS groups.

Exploring the relationship between the ecosystem service index and its specific components—carbon, fertility, and provision—and how the ecosystem services are linked to the AFS groups (Figure 11), it is evident that Low complexity AFSs exhibit a relatively inferior ecosystem services index, with an average of smaller dot sizes. Furthermore, it is noticeable that Medium and High complexity AFSs can be associated with soil fertility services or with carbon storage and provision depending on the location. Plots located in the Sixaola river basin tend to have higher soil fertility, while plots outside the Sixaola floodplain are more closely related to carbon storage and provision (Figure 11).

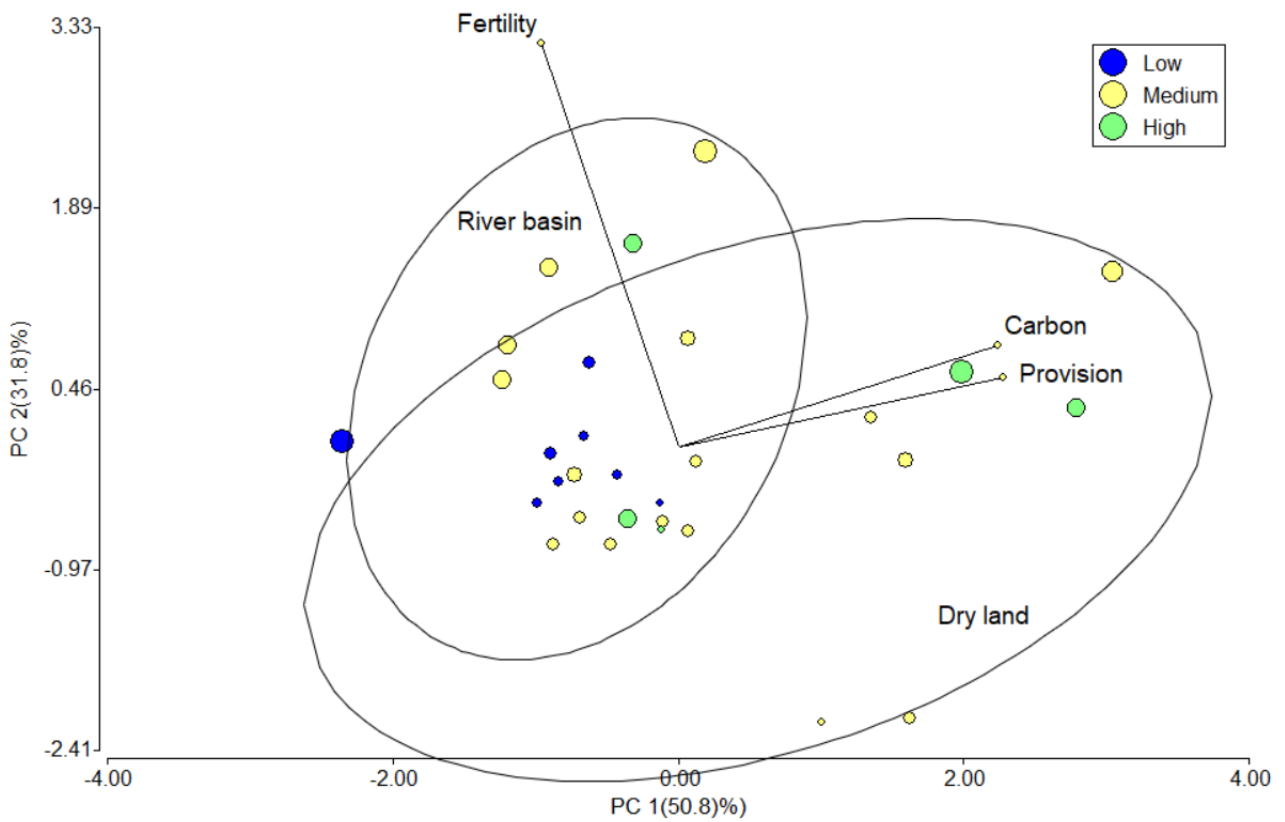


Figure 12: Relationship between the Ecosystem Service Composite Index (size of the circle), the ecosystem services type (soil fertility, aboveground carbon, and provision), and the AFS group. The location factor (river basin and dry land) are identified through the ellipsoids.

Table 8: Comparison of provision, carbon storage and soil fertility across ecological complexity AFS groups using Extended and Mixed Linear Models (F-value) and General Mixed Linear Models (Chi-square). Standard error is presented. n=30.

	Variable	F	Chi-sqr	p	Low	Medium	High
Provision	<b>*Cocoa yield (kg/ha.yr)</b>	<b>3.74</b>	-	<b>0.0368</b>	<b>892.66 ± 67.37 A</b>	<b>706.50 ± 49.52 B</b>	<b>632.40 ± 78.16 B</b>
	Cocoa yield (kg/tree.yr)	1.25	-	0.3021	1.35 ± 0.28 A	0.88 ± 0.09 A	0.97 ± 0.21 A
	<b>Fruit richness (trees/ha)</b>	-	<b>14.006</b>	<b>0.00091</b>	<b>1.75 ± 0.47 B</b>	<b>3.65 ± 0.46 A</b>	<b>5.60 ± 1.06 A</b>
	Timber density (trees/ha)	-	2.2895	0.3183	46.25 ± 20.27 A	107.06 ± 32.06 A	102.00 ± 56.32 A
	Fruit density (trees/ha)	-	0.66965	0.7155	46.25 ± 26.58 A	52.94 ± 20.86 A	92.00 ± 66.75 A
	<b>Musaceae density (trees/ha)</b>	-	<b>9.7425</b>	<b>0.007664</b>	<b>3.75 ± 2.82 B</b>	<b>127.65 ± 64.04 A</b>	<b>220.00 ± 203.43 A</b>
Carbon storage	Cocoa Carbon (Mg/ha)	2.42	-	0.1083	9.36 ± 0.99 A	7.20 ± 0.68 A	6.15 ± 1.26 A
	<b>** Shade tree Carbon (Mg/ha)</b>	<b>3.52</b>	-	<b>0.0437</b>	<b>17.22 ± 2.30 B</b>	<b>43.91 ± 9.19 A</b>	<b>58.22 ± 20.53 A</b>
	<b>*Total tree Carbon (Mg/ha)</b>	<b>5.49</b>	-	<b>0.01</b>	<b>26.59 ± 1.81 B</b>	<b>51.11 ± 8.89 A</b>	<b>64.38 ± 19.13 A</b>
Soil fertility	<b>*Soil Nitrogen (%)</b>	<b>7.8</b>	-	<b>0.0021</b>	<b>0.15 ± 0.03 B</b>	<b>0.22 ± 0.02 A</b>	<b>0.25 ± 0.03 A</b>
	*Soil Phosphorus (ppm)	1.9	-	0.1689	12.05 ± 1.24 A	7.86 ± 1.82 A	8.80 ± 4.54 A
	Soil Potassium (cm/kg)	0.67	-	0.5188	0.35 ± 0.06 A	0.36 ± 0.04 A	0.27 ± 0.07 A
	***Acidity (cmol/kg)	1.1	-	0.3461	0.12 ± 0.01 A	0.24 ± 0.06 A	0.15 ± 0.03 A
	<b>Soil organic Carbon (%)</b>	<b>3.49</b>	-	<b>0.045</b>	<b>1.56 ± 0.21 B</b>	<b>2.08 ± 0.14 A B</b>	<b>2.40 ± 0.26 A</b>
	*Fertility index	0.14	-	0.8728	2.20 ± 0.10 A	2.09 ± 0.19 A	2.13 ± 0.31 A
Total ecosystem service	Simple ES index	0.23	-	0.7965	1.22 ± 0.11 A	1.26 ± 0.09 A	1.34 ± 0.12 A
	<b>*Complete ES index</b>	<b>4.41</b>	-	<b>0.0219</b>	<b>1.26 ± 0.06 B</b>	<b>1.51 ± 0.10 A</b>	<b>1.73 ± 0.20 A</b>

\* Variable adjusted by the varIdent function.

\*\* Variables transformed by natural logarithm (ln).

\*\*\* Variables transformed to a rank, from 1 to 30.

\*\*\*\* Variables transformed by square root.

### 3.6 Relationship between the functional diversity and the production of ecosystem services in cocoa agroforestry systems

Through the exploratory analysis using PCA (Figure 11) with multiple variables conducted in this study, various associations can be observed. There is an inverse relationship between the total aboveground carbon and the cocoa productivity vectors. The total aboveground carbon, tree densities (except cacao density), shade, and most of the FD indices vectors are relatively large, representing the relevance of these parameters to explain the variability of this dataset. Conversely, cocoa productivity and nutrients had smaller vectors, indicating a minor association with this PCA.

Analyzing the CWMs, SLA, Hmax, LNC, and SLW, and LDMC vectors were the ones with a stronger association with the total aboveground carbon. Cocoa productivity presented an association with SSD, LDMC, LA, and also Raos Q and FDis. N and SOC were more associated with FDis, RaoQ, LNC, LPC, SLA, LA, Hmax, SSD, and LDMC. Cocoa productivity is associated with cacao density and is opposed to Musaceae density; it is also inversely related to shade. The total aboveground carbon was associated with timber density and shade percentage.

The relationships between them cannot be fully understood by this PCA, because it explains solely 49.8% of the data variability. Therefore, the regression models can give more precise information about how the FD and the ecosystem services interact.

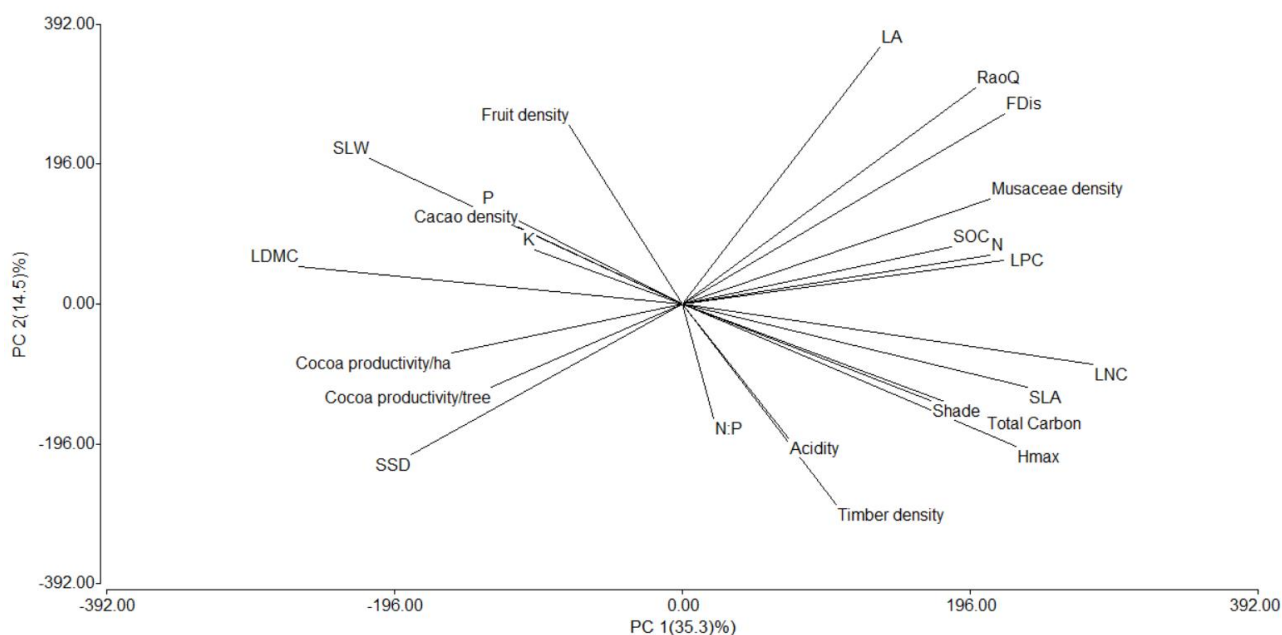
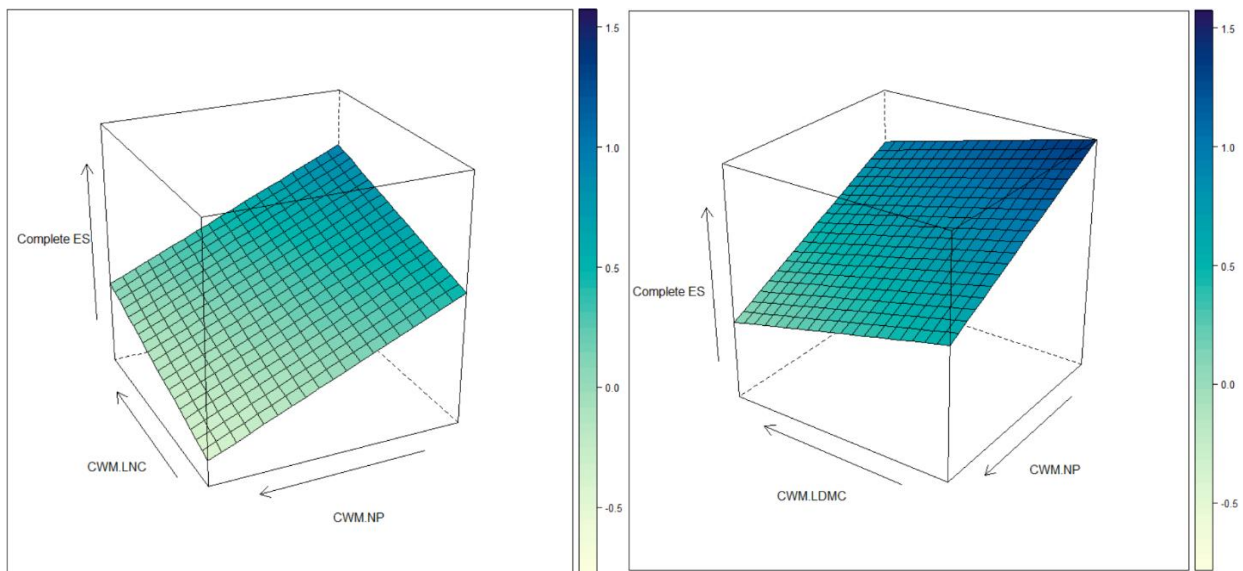


Figure 13: Principal component analysis including the functional indices, ecosystem services variables and AFS components densities.

The multiple regression analysis (Table 9) revealed several important and statistically significant relationships between abiotic and functional diversity variables and indicators of ecosystem services.

The Complete Ecosystem Service Index presented a significant negative relationship with LDMC and N:P, and a significant positive relationship with LNC (Figure 12). Together, these predictors explained 78% of the variability in the complete ecosystem service index, with N:P having the largest impact on the ecosystem services.



*Figure 14: 3D graphic illustrating the fixed coefficients of the linear model depicting relationships between the Complete Ecosystem Service Index and the Community Weighted Mean of Leaf Nitrogen Concentration (CWM LNC) and CWM Leaf Nitrogen and Phosphorus Ratio (CWM N:P) on the left figure. On the right figure, the same model for Complete Ecosystem Service Index presenting the relationships with the CWM of Leaf Dry Matter Content (LDMC) and Leaf Nitrogen and Phosphorus Ratio (N:P).*

The total aboveground carbon exhibited a significant positive relationship with CWM Hmax and a significant negative relation with CWM SLW, N:P, and FDis. These variables accounted for 84% of the variability in total carbon stock, with Hmax as the most influential predictor. Similarly, the shade tree carbon stock had an inverse relationship with CWM SLW and N:P and a significant positive relation with Hmax. This model explained 85% of shade tree carbon variability, with Hmax and N:P being the most important factors.

Cocoa yield per hectare was positively linked to potassium (K) levels and negatively associated with FDis. Together, these indices explained 31% of the variability in cocoa yield per hectare. When analyzing yield per tree, the predictors were shade percentage and leaf area (LA), which had significant negative relationships and accounted for 28% of the variability in cocoa yield per tree.

Both SOC and N had a significant and positive relation with the CWM LNC and soil clay proportion. These two independent variables were able to explain 66% of SOC variability and 70% of N variability, respectively, and clay proportion was the most important predictor for these variables. Phosphorus showed a negative relation with sand proportion, with a significant relationship with FD indices. This model accounted for 64% of phosphorus variability.

The soil fertility composite index showed a positive and significant relationship with clay and a significant and negative relationship with LDMC, which was the most influential predictor. None of the independent variables showed a significant relationship with K.

Overall, the results demonstrate important linkages between functional diversity attributes and key ecosystem services and soil properties in these cocoa AFSs. The predictive models explain substantial portions of variability across indicators, highlighting the utility of functional diversity for understanding ecosystem functioning.

Table 9: Resulting multiple regression models for ecosystem services proxies, with FD indices and abiotic parameters as independent variables, and with the random effect of location.

Predictor variable	Total aboveground Carbon			Shade trees Carbon			Cocoa yield per hectare			Cocoa yield per tree		
	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value
Constant	0.26	0.07	0.0009	0.29	0.08	0.0018	0.28	0.07	0.0005	0.46	0.050	<0.0001
<b>Soil abiotic variables</b>												
Shade	-	-	-	-	-	-	-	-	-	-0.21	0.050	0.0003
K	-	-	-	-	-	-	0.23	0.1	0.0347	-	-	-
<b>Community weighted mean (CWM)</b>												
SLW	-0.14	0.06	0.0206	-0.2	0.06	0.0034	-	-	-	-	-	-
Hmax	0.48	0.09	<0.0001	0.33	0.06	<0.0001	-	-	-	-	-	-
LA	-	-	-	-	-	-	-	-	-	-0.26	0.06	0.0001
N:P	-0.33	0.09	0.001	-0.32	0.1	0.0046	-	-	-	-	-	-
<b>Multi-trait index</b>												
FD <sub>is</sub>	-0.12	0.04	0.0077	-	-	-	-0.22	0.1	0.0304	-	-	-
R <sup>2</sup>	0.84			0.85			0.31			0.28		

Table 9: continuation.

Predictor variable	Nitrogen			Phosphorus			Soil organic carbon			Fertindex		
	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value	Coeff.	S.E.	p-value
Constant	-0.01	0.04	0.8604	0.4	0.22	0.0764	0.05	0.07	0.4945	0.51	0.21	0.0213
<b>Soil abiotic variables</b>												
Sand	-	-	-	-0.35	0.13	0.0107	-	-	-	-	-	-
Clay	0.51	0.060	<0.0001	-	-	-	0.58	0.1	<0.0001	0.28	0.13	0.0438
<b>Community weighted mean (CWM)</b>												
LDMC	-	-	-	-	-	-	-	-	-	-0.35	0.160	0.034
LNC	0.46	0.090	<0.0001	-	-	-	0.37	0.09	0.0003	-	-	-
R <sup>2</sup>	0.7			0.64			0.66			0.5		

Table 9: continuation.

Predictor variable	Complete Ecosystem Service		
	Coeff.	S.E.	p-value
Constant	0.84	0.2	0.0003
<b>Community weighted mean (CWM)</b>			
LDMC	-0.48	0.2	0.0256
N:P	-0.89	0.12	<0.0001
LNC	0.48	0.2	0.026
R <sup>2</sup>	0.78		



#### 4. Discussion

The average cocoa density found among all our studied plots was 756 trees per hectare, higher than the cocoa densities published by Cerda et al. (2014) for Costa Rica (592 trees/ha) and higher than the average cocoa density published by Somarriba et al. (2013) for Central America (545 trees/ha). The Musaceae density registered in our study, 183 plants/ha, was similar to Cerda et al. (2014) findings for Costa Rica (171 plants/ha), while Somarriba et al. (2013) found an average density of 117 stems per hectare in Central America. The average timber density in our study was 103 trees/ha, while Cerda et al. (2014) registered 67 trees/ha, and Somarriba et al. (2013) reported 104 trees/ha. The average fruit tree density in our samples was 78 trees/ha, while Cerda et al. (2014) found fruit densities of 36 trees/ha (excluding peach palm) in Costa Rica, and Somarriba et al. (2013) found, on average, 52 fruit trees/ha in Central America.

Another important parameter for AFS diagnosis is the basal area (BA), which serves as a proxy for tree size and biomass, supporting the evaluation of structural complexity and the development stage of the AFS. On average, the studied clonal cocoa AFSs presented a basal area of 24.5m<sup>2</sup>/ha, which is very similar to the average value reported for cocoa AFSs planted from seed in Costa Rica (Somarriba et al. 2013), which is 25.5m<sup>2</sup>/ha.

The ecological complexity also reflected differences in cocoa yield. In this research, the average yield was 760 kg/ha/year. The High complexity AFS groups, which presented the lowest average cocoa productivity among the AFS groups, produced 632 kg/ha/year. Comparing this to Costa Rica's average yield, the census from 2019 (not published) estimated the country's average yield at 265 kg/ha/year. Similarly, previous researchers estimated a low average yield for Costa Rica, at 146 kg/ha/year (Cerda et al. 2014). Therefore, our results showcase the higher genetic potential of clonal cocoa, which, together with the incorporation of regular pruning practices, can produce at least 2.9 times more than Costa Rica's average productivity.

From these comparisons between cocoa plantation densities, total tree basal area, and cocoa yields, it can be concluded that cocoa producers using clonal cocoa are managing higher tree stand densities and producing more cacao without reducing the total basal area from trees. This indicates that while cocoa yields may be intensified with clonal varieties, the overall shade tree cover and, as we further see, the generation of ecosystem services, are comparable to traditionally planted-from-seed cocoa AFSs.

Delving into the comparison of cocoa AFSs across a gradient of ecological complexity based on species richness, it is possible to observe that the AFS groups with contrasting ecological complexities also depict structural complexity differences. The significant differences in total tree density and shade tree density, contrasted with undifferentiated densities of the AFS components (except for Musaceae), denote an absence of patterns of consortiums and compositions specific to each AFS group. Therefore, regardless of the species richness, the AFS could be composed of relatively higher densities of timber or fruit trees or have a mixed composition (Table 8). The undifferentiation between the compositions of the AFSs strengthens our goal to analyze the specific effect of functional diversity, as composition patterns within the groups could lead to uncontrolled effects. Also, the undifferentiation in cocoa densities between the groups is ideal for our analysis because this sets the same basic condition for cocoa productivity in all the AFS groups.

The BA also showed relevant differences, with the Low complexity group presenting an average BA of 17.9m<sup>2</sup>/ha, while the Medium and High complexity AFSs presented 25.7m<sup>2</sup>/ha and 31.2m<sup>2</sup>/ha, respectively, surpassing the average BA from traditional cocoa AFSs in Costa Rica (Somarriba et al. 2013). Analyzing separately the BA from the shade tree component, the Low complexity AFSs presented levels below the theoretically optimal BA, and the Medium and High

complexity groups were above the optimal levels, according to Cerda et al. (2019), who propose a range of optimal shade tree BA from 10 to 15m<sup>2</sup>/ha in cocoa AFSs.

However, the functional diversity variables presented fewer significant differences across the gradient of ecological complexity. Four out of the eleven analyzed FD variables were significantly different across the AFS groups: the CWM LNC, LDMC, SSD, and to a lesser extent Hmax.

Therefore, we infer that AFSs with different ecological complexities based on their species richness also present different structural complexities, but not necessarily differ in their functional diversity. This implies that FD measures another dimension from the biodiversity in AFSs that is not properly described by the traditional analytical strategies.

Nevertheless, the detected differences in functional diversity across the gradient of ecological complexity are highly relevant. These functional indices are key variables related to resource use strategies. The variation in these traits allocates the species along the plant economic spectrum, characterizing them as acquisitive-resource-use or conservative-resource-use plants. Acquisitive plant strategists are associated with fast rates of ecosystem processes, such as rapid decomposition of their nutritionally rich leaves and efficient primary productivity with a reduced cost of leaf construction, resulting in a competitive ability due to faster resource acquisition (Cornwell et al. 2008). In natural succession, they dominate during early succession stages (Han et al. 2023). Conservative plant strategists, on the opposite side of the trait spectrum, have a conservative use of resources and slower growth (Carreño-Rocabado et al. 2012, Reich 2014, Maracahipes et al. 2018); in natural forests, they are part of later succession stages (Han et al. 2023).

The differences in functional diversity observed among AFS groups with contrasting ecological complexity conditions represent distinct ecological strategies, allocating them to opposite sides of the acquisitive-conservative, or fast-slow, axis. The Low complexity groups, with lower values of LNC and higher LDMC and SSD, can be classified as slow-conservative AFSs, while the Medium and High complexity AFS groups can be considered as fast-acquisitive AFSs. Applying the acquisitive and conservative or fast and slow terminology to AFSs is helpful because it provides a straightforward way to refer to a range of traits that define the ecological processes within AFSs.

The ecosystem services were associated with the functional diversity patterns of contrasting ecological strategies detected across the AFS groups. On average, the studied plots had 46.78Mg/ha of carbon, which is similar to the results from Somarriba et al. (2013) for Costa Rica and Central America, reported as 52.7Mg/ha and 49.2Mg/ha ( $\pm$ SD), respectively. This is also comparable to carbon stocks in cocoa AFSs on other continents (Isaac et al. 2005). However, the carbon stocks exhibited wide variability across the AFS groups, ranging from 17.84 to 149.13Mg/ha. The slow-conservative-Low complexity group had lower carbon stocks, while the faster-acquisitive-Medium and High complexity groups had higher carbon stocks, reflecting the dominant trait in each AFS group.

The different ecological strategies across the groups also manifested in differences in soil chemical fertility, as the faster-acquisitive Medium and High complexity AFS groups enhanced soil fertility through their fast growth and decomposition of leaves (Salgado-Negret 2016, Gorné et al. 2022). This resulted in higher concentrations of soil nitrogen and soil organic carbon (SOC) in these two complex AFS groups. Such a relationship between the functional diversity composition of shade trees and soil fertility in cocoa AFSs is supported by previous publications (Sauvadet et al. 2020). Therefore, in terms of aboveground carbon and nutrient fertility, it can be concluded that the Medium and High complexity groups are more dynamic, producing more carbon and making important nutrients more available.

However, more complex systems are not necessarily superior in all aspects. The Medium and High complexity groups had significantly lower cocoa yields per hectare than the Low complexity group, suggesting a tradeoff between ecosystem services of carbon storage and soil fertility and cocoa provision, as reported in previous investigations (Blaser et al. 2018). Nevertheless, when the cocoa tree density per hectare is taken into account, the cocoa yield per tree showed no significant differences across the groups.

For an ecosystemic approach, considering that different ecological processes occur at various spatial scales (Lindborg et al. 2017), the hectare serves as a unit for landscape-scale ecosystem analysis. Additionally, it supports farmers in optimizing their resources within the constraints of a limited property area. However, analyzing on a per-tree basis provides a better perspective on plant ecophysiology, revealing how a cocoa tree responds to environmental conditions.

These inconsistent results indicate that cacao yield is not completely associated with the ecological complexity of AFSs. At a landscape level, the low complexity AFSs had a better productive performance, but at an ecophysiological level these clonal cocoa trees maintained the production regardless of the ecosystem conditions.

When analyzing all these environmental services together, there was no difference between the groups for the Simple Ecosystem Services Index, which includes only cocoa production as provisioning. However, significant differences were observed between the groups for the Complete Ecosystem Service Index, which contemplates the potential contribution of timber and fruit to ecosystem provisioning. The result from the Simple Ecosystem Service Index reinforces the existing presumption of tradeoffs between ecosystem services generated by trees and cocoa production (Blaser et al. 2018, Ruf 2011). On the other hand, the result from the Complete Ecosystem Service Index follows the logic of the Land Equivalent Ratio, considering that the contribution of multiple agroforestry system components can counterbalance the reduction of cocoa yield caused by intercropping. This result suggests that it is possible to achieve a win-win scenario—positive for carbon, soil chemical fertility, and provisioning—when the shade trees are productive and can generate benefits. Otherwise, it is more likely to be a tradeoff between ecosystem services.

Timber and fruit trees have the potential to generate more income than cocoa itself in cocoa agroforestry systems (Cerdeira et al. 2014, Ramírez-Argueta et al. 2022). Therefore, it is important to improve methods for estimating yields from these components in farm conditions, as producers often do not keep records or may be hesitant to share information (Wiseman et al. 2019). In this research, we used timber and fruit tree densities as proxies for their respective potential productivities. However, obtaining actual quantifications or estimations of the total harvest would provide a more accurate understanding of the dynamics of timber and fruit components in agroforestry systems.

In summary, the characterization of functional diversity along a gradient of ecological complexity in AFS groups demonstrates that the Low ecological complexity group exhibited predominantly conservative traits, while the Medium and High ecological complexity groups displayed predominantly acquisitive traits. These trait profiles imply slower biomass growth and nutrient availability in the Low complexity group, and faster biomass growth and nutrient availability in the Medium and High complexity groups. This difference in trait profiles may be associated with different production strategies. Producers in the Low complexity group may not be interested in the benefits from the trees and may focus solely on cocoa productivity, whereas producers in the Medium and High complexity groups seek multiple outcomes from their AFS.

Based on the multiple regression model analysis, seven out of the nine functional indices, which included both the CWM and multi-trait indices, showed significant effects on ecosystem services.

Specifically, the CWM indices, including Hmax, SLW, LA, LNC, N:P, LDMC, and FDis, demonstrated stronger predictive power for ecosystem services compared to the multi-trait indices. Notably, the multi-trait indices were only significant for cocoa yield per hectare and total aboveground carbon.

As anticipated, AFSs dominated by tall trees (Hmax) exhibit higher carbon stocks, aligning with patterns observed in natural forests (Conti and Díaz 2013, Finegan et al. 2015). Furthermore, in AFSs, the Community-Weighted Means (CWM) SLW was inversely correlated with carbon stock increments. This inverse relationship is attributed to the acquisitive nature of AFSs with low SLW, which facilitates faster growth and carbon stock accumulation from an early stage. Additionally, the leaf N:P ratio emerged as a significant predictor of total carbon stocks, displaying an inverse relationship. This finding aligns with patterns observed in natural forests (Finegan et al. 2015). In the context of these cocoa AFSs, the N:P ratio is inversely associated with high leaf phosphorus concentration (LPC) (refer to traits in the appendix). Consequently, in situations where shade trees are scarce, and there is a prevalence of cacao traits characterized by small height and low LPC, resulting in low CWM Hmax, high CWM N:P, and consequently, low carbon stocks due to the absence of shade trees. This elucidates why functional dispersion (FDis) is also a crucial predictor, exhibiting an inverse relationship with total aboveground carbon. When FDis is low, traits are less dispersed and can be concentrated in specific functions that augment carbon stocks.

Quesada et al. (2012) postulated that soil variables, specifically soil phosphorus, are the most important factor for forest growth. In the AFSs we found contrasting evidence. Even though phosphorus was deficient in many of the soil samples, the biotic variables were more determinant for carbon stocks (Table 9).

These findings suggest that in order to maximize carbon storage in these cocoa AFSs, it is recommended to select shade tree species with a composition of traits involving of high trees (Hmax), low leaf N:P ratio (which implies high LPC), and light density leaves (SLW). At a community level, reducing the functional differences (having low FDis) by enhancing large trees dominance also increases the carbon storage potential.

Significant relationships were observed between soil fertility parameters and soil texture. Clay proportion exhibited a positive influence on N, SOC, and overall fertility (Ferindex), while sand had a negative impact on phosphorus availability. Higher CWM LNC positively influenced N and SOC, whereas CWM LDMC negatively affected overall fertility. This trait syndrome resembles that of resource-acquisitive plants and supports the principle that leguminous trees, characterized by high LNC, enhance soil chemical fertility (Epihov et al. 2021). In contrast, cocoa possesses low LNC and relatively high LDMC. Thus, AFSs incorporating shade trees with dissimilar traits from cocoa contribute to improved soil functions. This suggests that the interaction between shade trees and cocoa generates a positive effect on soil fertility when these components have contrasting leaf traits. The association between contrasting traits in cocoa and shade trees, and the resulting resource complementarity, has been explored in previous studies, considering phylogenetic differences (Sauvadet et al. 2020) and dissimilarities in leaf litter traits (Sauvadet et al. 2020).

The cocoa yield exhibited a positive correlation with K, as extensively documented in the literature (Hartemink 2005). However, a noteworthy negative relationship was observed with FDis. This finding suggests that AFSs characterized by a consortium with contrasting functional traits tend to yield lower cocoa outputs. This correlation aligns with the logical expectation, given that in a cocoa AFSs, cocoa stands out as the dominant species, constituting the majority of the relative basal area in the plots. In such a scenario, systems with a low relative basal area of shade trees have their average traits and ecological functions primarily influenced by cacao. Higher FDis, which adversely impacts cocoa yield per hectare, is contingent on a greater basal

area from shade trees possessing dissimilar traits from cacao. This dissimilarity leads to competitive interactions between these components. Consequently, a system with low FDis, indicative of higher cocoa yield per hectare, essentially signifies a system with cacao predominance, akin to the Low complexity AFS groups described earlier. In this context, FDis serves as a surrogate for shade percentage or shade tree density. Our results highlight that FDis is more significantly correlated with cocoa yield per hectare than these traditional proxies. Thus, FDis emerges as a valuable indicator, providing insights into the competitive dynamics within agroforestry systems and their impact on cocoa productivity.

On the other hand, the cocoa yield per tree was explained by shade percentage and CWM LA, with negative relation with both variables (Table 9). This finding means that the average cocoa tree yield increases when shade is controlled, especially the shade from plants with large leaf areas, keeping the shade percentage around 30% (Table 7), as reported by several studies (Somarriba et al. 2018, Blaser et al. 2018).

Our analysis of cocoa yield results reveals that diverse management strategies can enhance productivity. Comparative models suggest that optimizing cocoa yield per hectare involves reducing species richness and structural complexity, while maintaining a low mass ratio of acquisitive species and ensuring specific leaf traits, such as low LDMC and SSD and high LNC (Tables 7 and 9). Multiple regression models indicate that improving cocoa yield is associated with reducing dispersion (FDis) by controlling shade tree influence, increasing soil potassium (K), and adopting practices like reducing shade percentage and average leaf area. Crucially, these strategies are not mutually exclusive, showing that fertilizing with K and managing shade percentage can increase cocoa yield without sacrificing ecosystem complexity (Table 9). In essence, when the shade canopy is competitively efficient in resource acquisition, it can coexist with cacao, resulting in elevated shade levels conducive to higher cocoa yields.

To evaluate multifunctionality in AFSs, we included the environmental services of carbon storage, soil fertility, and provision in one single variable, the Complete Environmental Service Index. We found that the most important variables to predict multifunctionality in an AFS were the leaf traits, LNC, N:P ratio, and LDMC. As we may assume based on the models of single environmental services (carbon storage, nutrient fertility), LNC and LDMC are associated with soil fertility, and LNC and N:P are associated with carbon storage. Provisioning that includes cacao yield, but also fruit and timber tree densities, we presume is associated with growth response traits, the same traits that affect carbon storage, as suggest Figure 11. This trait syndrome suggests that AFSs can maximize their multiple ecosystem services when they are composed by acquisitive shade tree species, with high LNC and low LDMC, and by species with low N:P and high LPC (Figure 12). This corresponds to increases in provisioning when the benefits from timber and fruit trees are utilized.

Timber yields represent important resources in cocoa AFSs, either providing a source of cash flow or serving as a financial asset. In Central America, these yields can contribute significantly, with an annual potential of 265 US\$/ha (Somarriba et al. 2014). However, many producers are currently not capitalizing on this valuable resource. The haphazard planting of shade trees in cocoa AFSs poses challenges for future harvests, as the impact of tree falls on cocoa trees can hinder effective management of the main crop. Consequently, if shade trees are left unmanaged and unharvested, producers miss out on potential additional income and may experience adverse effects on cocoa yield due to excessive shading and other associated factors (Blaser et al. 2018). To address this issue, Esche et al. (2023) propose subsidizing shade tree pruning as a means to integrate shade tree cover in productive AFSs. Another viable strategy to support cocoa producers in maintaining shade tree cover is the implementation of payment for environmental services, as suggested by Dominicis et al. (2023).

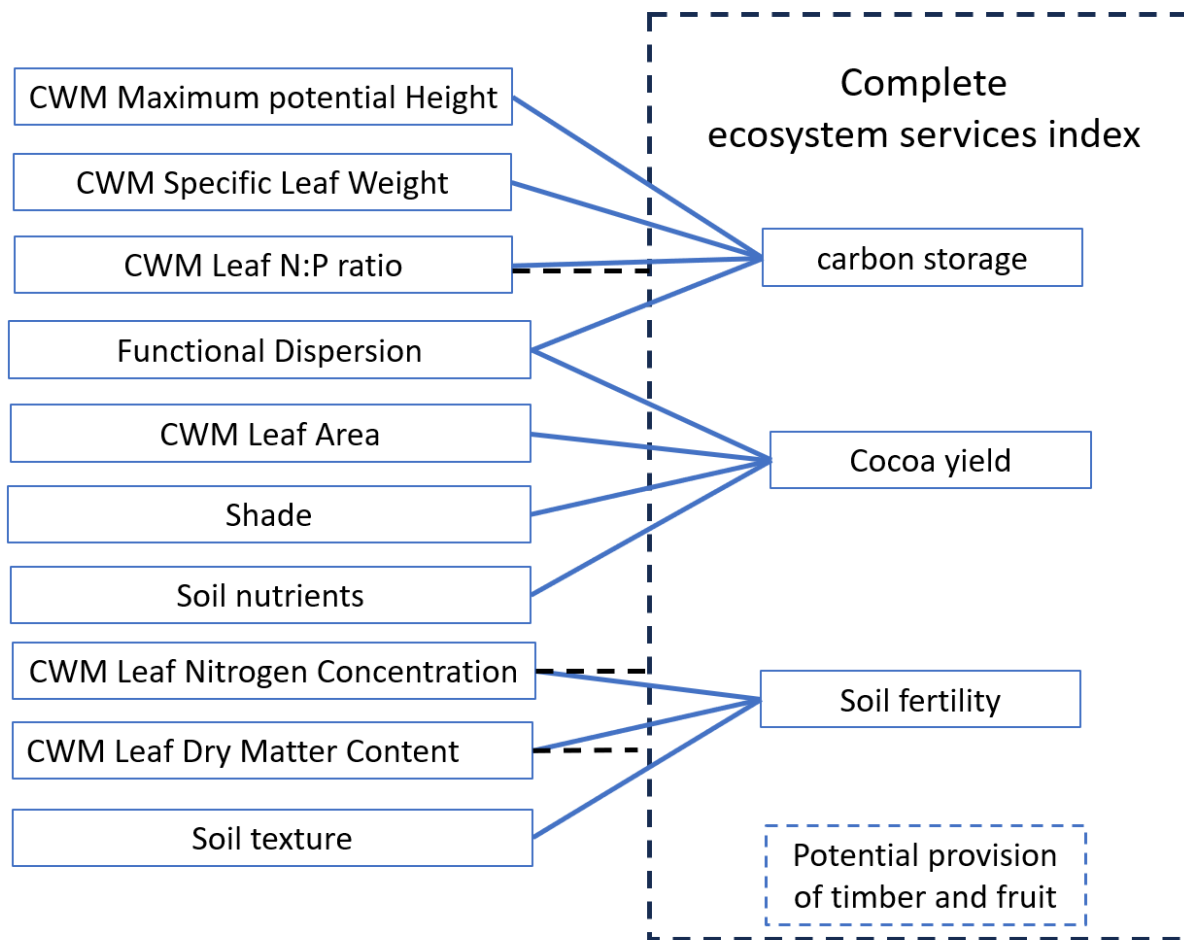


Figure 15: Scheme of the multiple regression models from the effect abiotic factors and functional diversity indices on ecosystem services. Blue lines represent the significant covariation between independent variables (abiotic variables: soil texture, soil nutrients, shade; and community weighted mean of: maximum potential height,  $H_{max}$ ; Specific Leaf Weight,  $SLW$ ; Leaf Nitrogen-Phosphorus Ratio,  $N:P$ ; Leaf Nitrogen Concentration,  $LNC$ ; Leaf Dry Matter Content,  $LDMC$ ; Leaf Area,  $LA$ ; functional dispersion,  $FDis$ ) and ecosystem services. The dashed line represents the significant relations with Complete Ecosystem Service Index, that also includes the potential provision from timber and fruit trees.

The statistical methods employed in this study yielded consistent evidence. The ANOVA analysis, which compared AFS groups with varying levels of ecological complexity, revealed significant associations with high shade tree richness, dense shade tree populations, and specific functional indices and trait syndromes. Likewise, the regression models examining the impact and response of functional diversity on ecosystem service variables demonstrated correlations with carbon stocks, nutrient fertility, and the outcomes related to cocoa yield and the overall AFS provision. These findings underscore the influence of shade tree characteristics and functional traits on the ecological dynamics and services provided by AFSs.

No conflicts were observed among the functional indices across various ecosystem services, indicating a lack of tradeoffs. These indices were consistently linked to the generation of ecosystem services, with functional traits associated with acquisitive species proving to be the most promising for generating multiple services. Notably, the trait variation represented by  $FDis$  was crucial in highlighting that communities with low  $FDis$  can concentrate functional traits,

leading to specific effects and responses, such as enhanced carbon storage and increased cocoa yield. This underscores the importance of understanding trait variation in shaping the multifunctionality of ecosystems.

In summary, we found that AFSs characterized by "fast"-acquisitive traits, where species with low SLW, LDMC, N:P, and high LNC, Hmax dominate the mass ratio, prove advantageous for enhancing multiple ecosystem services. We identified a tradeoff between ecosystem services and cocoa productivity, yet this tradeoff can be transformed into a win-win scenario by strategically utilizing resources from timber and fruit trees. Achieving this balance becomes particularly effective when the composition of shade trees includes acquisitive species, emphasizing the potential for harmonizing cocoa productivity with broader ecosystem service goals.

To advance our understanding in this field, it is crucial to analyze the impact of functional diversity on the financial performance of AFSs, incorporating measured or estimated yields of AFS products. This approach can provide farmers with a more solid foundation for making informed management decisions. Additionally, refining functional diversity models for cocoa AFSs is essential, and integrating more ecosystem services critical for cocoa production and human well-being is paramount. An illustrative example is the association between functional diversity and the control of pests and pathogens (Gagliardi et al. 2021). Depending on local conditions and environmental boundaries, other ecosystem services may gain relative importance, such as erosion control, water retention, temperature regulation, and providing habitat for insects. A comprehensive analysis considering these factors would contribute significantly to optimizing the performance of cocoa AFSs.

## 5. Conclusion

In cocoa Agroforestry Systems (AFSs) featuring grafted clones from CATIE, the gradient of ecological complexity based on species richness was succeeded by an ascending trend in tree densities, basal area, and shade percentage. These shifts in ecological complexity were accompanied by corresponding changes in functional diversity, influencing the Community Weighted Mean (CWM) of Leaf Dry Matter Content (LDMC), Leaf Nitrogen Concentration (LNC), Specific Stem Density (SSD), and Maximum Potential Height (Hmax). Variations in these functional traits across the AFSs reflect distinct ecological strategies. AFSs with medium and high ecological complexity were dominated by acquisitive species, characterized by low LDMC and SSD and high LNC, exhibiting fast leaf turnover and high photosynthetic capacity that foster rapid growth (Gorné et al. 2022), designating them as fast-AFSs with more dynamic carbon and nutrient cycling. Conversely, AFSs with low ecological complexity were dominated by conservative species, featuring high LDMC and SSD and low LNC, indicating resource conservation through low matter turnover and slower growth (Gorné et al. 2022), categorizing them as slow-AFSs with less dynamic carbon and nutrient cycling. Despite these distinctions, most functional indices remained unaffected by ecological complexity, suggesting that traditional variables like species richness and structure cannot fully capture the functional dimension. Therefore, the characterization of functional diversity in AFS complements traditional variables, offering a more comprehensive assessment of the ecological processes performed by AFSs.

The contrasting ecological conditions along the complexity gradient resulted in distinct ecosystem properties. AFSs with low ecological complexity, associated with "slow" conservative traits, exhibited the lowest carbon stocks and soil fertility. Despite having higher cocoa yields per hectare, no significant differences were detected in cocoa yield per tree. In contrast, AFSs with medium and high ecological complexity, characterized by "fast" acquisitive traits, stored larger amounts of carbon, displayed higher soil chemical fertility, and yielded less cocoa per hectare. However, these systems

achieved the same yields per tree as low-complexity AFSs, with the added benefit of enhancing other environmental services.

The total carbon stocks and shade tree carbon stocks exhibited correlations with the Community Weighted Mean (CWM) of Maximum Potential Height (Hmax), Specific Leaf Weight (SLW), and Leaf Nitrogen-Phosphorus Ratio (N:P). Soil fertility in cocoa AFSs showed associations with soil texture, CWM Leaf Nitrogen Concentration (LNC), and CWM Leaf Dry Matter Content (LDMC). Cocoa yield was linked to soil potassium (K), Functional Dispersion (FDis), Leaf Area (LA), and shade percentage. Multiple ecosystem services, encompassing carbon storage, soil chemical fertility, and the provision of cocoa, fruits, and timber, were connected to CWM LNC, CWM N:P, and CWM LDMC.

To optimize specific ecosystem services, it is advisable to design the AFS with species possessing particular functional traits that contribute to the desired outcomes. For maximizing carbon storage in AFS shade trees, it is recommended to have low variability of functional traits (low FDis), predominantly composed of tall trees (Hmax), high LNC, and low Specific Leaf Weight (SLW). To enhance soil chemical fertility, the shade trees should consist of species with high LNC and low LDMC. In general, to maximize carbon storage or soil chemical fertility in cocoa AFSs, incorporating acquisitive species that exhibit rapid growth, sequestering substantial carbon quantities, and having easily decomposable soft tissues can prove beneficial in enhancing soil fertility.

The commercialization of cocoa stands as the primary source of income in the studied AFSs. Consequently, the economic sustainability of cocoa AFSs and the perpetuation of all associated environmental services hinge on achieving satisfactory cocoa productions. To enhance cocoa provision, it is highly advisable to prioritize the cultivation of grafted cocoa from improved varieties. Plantations featuring CATIE cocoa clones yielded at least three times more than those with traditional hybrids. Additionally, we discovered that cocoa productivity can be further increased through effective management practices. These include shade control, especially from plants with large LA, the application of K amendments, and the regulation of functional traits variability among trees (FDis). This involves reducing the dominance of acquisitive shade trees with functional traits dissimilar to cacao, thereby contributing to improved cocoa yields.

The win-win scenario, wherein multiple ecosystem services are enhanced, becomes achievable through the utilization of fruit and timber trees. To maximize a range of ecosystem services, we propose the inclusion of shade trees characterized by high Leaf Nitrogen Concentration (LNC), low Leaf Dry Matter Content (LDMC), low Leaf Nitrogen-Phosphorus Ratio (N:P), and high Leaf Phosphorus Concentration (LPC). An ideally balanced AFS consortium exhibiting these traits should incorporate acquisitive species such as *Leucaena leucocephala*, *Shilozobium parahyba*, *Erythrina poeppigiana*, among other leguminous and non-leguminous trees (Figure 4).

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## 7. Appendix

Table 10: Allometric equations utilized to estimate aboveground carbon.

Species	Equation	Source
Anacardium excelsum	$\ln(B) = -3.7179 + 2.1936 \cdot \ln(\text{dap}) + 0.4132 \ln(H)$	Losi, et al. 2003
Fruit trees	$\ln(B) = -2.57 + 2.65 \cdot \ln(\text{DBH})$	Andrade, H.J., Segura, M. & Somarriba, E. 2022
Artocarpus heterophyllus	$\text{AGB} = \text{EXP}(-0.897 + 1.990 \cdot \ln(\text{DBH}))$	Sandra Brown, Andrew J. R. Gillespie, Ariel E. Lugo 1989
Bactris gasipaes	$\text{AGB} = 0.74 \cdot H^2$	Szott, L.T., Arévalo-López, L.A., Pérez, J., 1993
Carica papaya	$\text{AGB} = 1.282 \times (7.7H + 4.5)$	Aguaron E, McPherson EG, 2012
Cecropia sp.	$\text{AGB} = 12.764 + 0.2588 \cdot \text{DBH}^{2.0515}$	Pearson et al, 2016.
Cedrela odorata	$\text{AGB} = 0.0013 \cdot (\text{DBH}^2) \cdot (H^{0.9218}) + 0.0072 \cdot (\text{DBH}^2) \cdot (H^{1.0451}) + 0.0029 \cdot (\text{DBH}^2) \cdot (H^{1.0172}) + 0.0010 \cdot (\text{DBH}^2) \cdot (H^{0.8038})$	Thomas G. Cole, John J. Ewel, 2006
Cedrela odorata	$\text{AGB} = 0.0673 \cdot (\rho \cdot \text{DBH}^2 \cdot H)^{0.976}$	Chave, 2014.
Cocus nucifera	$\text{AGB} = \text{EXP}(-3.3488 + (2.7483 \cdot \ln(\text{DBH})))$	Goodman, R. et al. 2013.
Cordia alliodora	$\text{AGB} = -2.7 + 2.49 \cdot \ln(\text{DBH})$	Andrade, H.J., Segura, M. & Somarriba, E. 2022
Dypterix panamensis	$\ln(\text{AGB}) = -3.011 + 2.947 \cdot \ln(\text{DBH})$	Montero, M. M. and Montagnini, F. 2004.
Erythrina fusca, Gliricidia sepium	$\text{AGB} = (21.3 - 6.95 \cdot (\text{DBH}) + 0.74 \cdot (\text{DBH}^2))$	Brown, S.; Iverson, L.R. 1992.
Inga edulis	$\text{Log}(\text{AGB}) = -0.889 + 2.317 \cdot (\text{Log}(\text{DBH}))$	Segura et al, 2006
Musa	$\text{AGB} = 0.0303 \cdot D^{2.1345}$	Van Noordwijk M, Mulia R., 2002
Persea americana	$\text{AGB} = 10^{(-1.11 + 2.64 \cdot \text{Log}_{10}(\text{DBH}))}$	Andrade, H.J.; Segura, M.; Somarriba, E.; Villalobos, M. 2008
Tabebuia rosea	$\text{AGB} = 0.1959 \cdot (\text{DAP}^{2.1206})$	Návar, J., 2009
Terminalia oblonga	$\text{Log}(\text{AGB}) = -2.538 + 2.614 \cdot \text{Log}(\text{DBH})$	Montero, M. M. and Montagnini, F. 2004.
Zanthoxylum riedelianum	$\text{AGB} = (0.00166 \cdot (\text{DBH})^{3.6586})$	Manzano, F. 2010
All other trees	$\text{AGB} = 0.0673 \cdot (\rho \cdot D^2 \cdot H)^{0.976}$	Chave, 2014.

Table 11: Trait values assumed for each of the dominant species.

Species name	SSD	SLA	LDMC	LA	SLW	Hmax	LNC	LPC	NP
Anacardium excelsum	0.41	8.71	397.82	28104.60	0.11	35.11	16.60	1.50	11.04
Annona papilionella	0.32	13.01	411.76	5219.60	0.08	32.50	26.65	1.59	16.81
Bactris gasipaes	0.70	9.50	397.60	25531.20	0.11	18.00	25.50	1.30	19.62
Citrus spp	0.74	11.10	338.71	2607.40	0.09	10.00	16.70	0.56	29.82
Cordia alliodora	0.55	12.99	362.90	7274.70	0.08	35.00	31.50	1.34	23.55
Chrysophyllum cainito	0.61	6.94	463.16	3736.30	0.14	20.00	19.00	1.00	19.00
Chloroleucon eurycyclum	0.62	14.49	453.83	14367.10	0.07	27.19	47.80	1.70	28.12
Cocos nucifera	0.50	4.81	657.51	1786172.20	0.21	32.88	11.90	1.60	7.44
Cedrela odorata	0.45	14.10	434.59	61279.20	0.07	33.53	28.97	2.03	14.26
Erythrina poeppigiana	0.31	25.94	221.81	38241.50	0.04	35.00	50.80	1.38	36.89
Hyeronima alchonoides	0.63	11.59	311.59	18658.65	0.09	28.50	25.11	1.16	21.65
Hura crepitans	0.38	16.32	280.10	10705.10	0.06	35.00	36.00	3.70	9.73
Inga edulis	0.59	11.68	500.00	37718.10	0.09	17.00	28.52	1.60	17.82
Leucaena leucocephala	0.68	23.08	332.44	19277.60	0.04	16.00	38.50	1.50	25.67
Luehea seemannii	0.56	12.71	465.84	9181.60	0.08	30.00	20.30	1.16	17.56
Musa spp	0.04	14.48	219.76	949731.00	0.07	5.20	39.50	2.30	17.17
Mangifera indica	0.55	7.01	428.57	6609.00	0.14	20.00	16.00	1.41	11.33
Nephelium lappaceum	0.71	8.00	465.47	18343.30	0.12	20.00	18.30	2.80	6.54
Persea americana	0.50	10.68	437.11	9114.80	0.09	20.00	17.70	0.83	21.33
Spondias dulcis	0.37	20.08	183.01	29657.80	0.05	22.00	17.60	1.50	11.73
Sapium glandulosum	0.47	10.39	358.78	5779.10	0.10	33.81	21.21	1.68	12.64
Spondias mombin	0.43	14.52	319.01	43860.40	0.07	27.00	19.40	1.10	17.62
Shizolobium parahyba	0.44	12.39	431.86	158999.30	0.08	30.00	40.87	1.40	29.20
Spondias purpurea	0.36	19.23	215.09	9120.50	0.05	9.00	20.89	1.08	19.28
Theobroma cacao	0.41	12.47	415.28	29369.10	0.08	8.00	19.23	0.77	25.11
Terminalia oblonga	0.73	12.26	451.61	6362.80	0.08	37.50	23.43	1.90	12.33
Tabebuia rosea	0.53	8.01	435.69	55221.30	0.12	30.70	15.14	0.95	15.87
Zanthoxylum riedelianum	0.48	11.48	408.48	81411.30	0.09	30.00	22.21	1.46	15.16

Table 12: Trait values measured from cocoa AFS dominant species in Caribbean Huetar, Costa Rica.

Specie	Trait name	Acro- nym	Unit	n	Average	error.std	Min	Max
Anacardium excelsum	Leaf area	LA	mm <sup>2</sup>	25	28391.680	1630.735	13362.100	44836.900
Anacardium excelsum	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	8.869	0.140	7.947	10.844
Anacardium excelsum	Leaf dry matter content	LDMC	mg/g	30	398.136	6.755	312.579	472.946
Anacardium excelsum	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.113	0.002	0.092	0.126
Annona pittieri	Leaf area	LA	mm <sup>2</sup>	25	5773.072	357.736	3511.900	10217.000
Annona pittieri	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	13.180	0.236	10.817	15.388
Annona pittieri	Leaf dry matter content	LDMC	mg/g	25	409.006	5.363	373.333	482.759
Annona pittieri	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.076	0.001	0.065	0.092
Cedrela odorata	Leaf area	LA	mm <sup>2</sup>	25	69524.072	5539.777	40762.500	168765.600
Cedrela odorata	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	14.505	0.588	10.006	21.650
Cedrela odorata	Leaf dry matter content	LDMC	mg/g	25	441.263	16.876	311.526	580.972
Cedrela odorata	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.072	0.003	0.046	0.100
Chloroleucon eurycyclum	Leaf area	LA	mm <sup>2</sup>	25	18381.648	1985.456	5073.600	38174.800
Chloroleucon eurycyclum	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	16.046	0.700	12.637	25.004
Chloroleucon eurycyclum	Leaf dry matter content	LDMC	mg/g	25	458.740	10.588	328.090	588.608
Chloroleucon eurycyclum	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.065	0.002	0.040	0.079
Chrysophyllum cainito	Leaf area	LA	mm <sup>2</sup>	28	3763.350	166.926	2190.900	5490.900
Chrysophyllum cainito	Specific leaf area	SLA	mm <sup>2</sup> /mg	28	6.704	0.192	5.014	9.178
Chrysophyllum cainito	Leaf dry matter content	LDMC	mg/g	28	469.440	6.163	387.755	535.714
Chrysophyllum cainito	Specific leaf weight	SLW	mg/mm <sup>2</sup>	28	0.152	0.004	0.109	0.199
Citrus spp	Leaf area	LA	mm <sup>2</sup>	30	2759.623	182.381	1366.700	5856.300
Citrus spp	Specific leaf area	SLA	mm <sup>2</sup> /mg	30	11.544	0.341	9.150	16.713
Citrus spp	Leaf dry matter content	LDMC	mg/g	30	339.658	3.889	302.326	383.333
Citrus spp	Specific leaf weight	SLW	mg/mm <sup>2</sup>	30	0.089	0.002	0.060	0.109
Cocos nucifera	Leaf area	LA	mm <sup>2</sup>	9	2133431.244	168613.601	1595502.900	2752333.900
Cordia alliodora	Leaf area	LA	mm <sup>2</sup>	25	7315.152	592.159	1835.600	13273.500

<i>Cordia alliodora</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	14.047	0.763	9.149	22.746
<i>Cordia alliodora</i>	Leaf dry matter content	LDMC	mg/g	25	375.687	12.880	268.908	493.151
<i>Cordia alliodora</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.076	0.004	0.044	0.109
<i>Erythrina poeppigiana</i>	Leaf area	LA	mm <sup>2</sup>	25	41351.392	2654.205	17013.600	67986.600
<i>Erythrina poeppigiana</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	25.965	1.446	14.178	41.393
<i>Erythrina poeppigiana</i>	Leaf dry matter content	LDMC	mg/g	25	237.856	9.275	163.606	329.287
<i>Erythrina poeppigiana</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.042	0.002	0.024	0.071
<i>Luehea seemannii</i>	Leaf area	LA	mm <sup>2</sup>	25	8822.936	511.844	3639.700	15119.900
<i>Luehea seemannii</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	12.991	0.477	9.361	17.934
<i>Luehea seemannii</i>	Leaf dry matter content	LDMC	mg/g	25	477.098	8.745	430.233	572.519
<i>Luehea seemannii</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.079	0.003	0.056	0.107
<i>Hura crepitans</i>	Leaf area	LA	mm <sup>2</sup>	25	10871.956	725.863	5992.500	23566.700
<i>Hura crepitans</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	16.412	0.570	12.398	23.414
<i>Hura crepitans</i>	Leaf dry matter content	LDMC	mg/g	25	292.383	9.111	218.623	372.340
<i>Hura crepitans</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.063	0.002	0.043	0.081
<i>Hyeronima alchonoides</i>	Leaf area	LA	mm <sup>2</sup>	30	18804.933	1112.662	10188.700	33804.400
<i>Hyeronima alchonoides</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	30	11.635	0.198	9.518	14.263
<i>Hyeronima alchonoides</i>	Leaf dry matter content	LDMC	mg/g	30	312.335	4.434	263.158	359.629
<i>Hyeronima alchonoides</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	30	0.087	0.001	0.070	0.105
<i>Inga edulis</i>	Leaf area	LA	mm <sup>2</sup>	25	39199.964	2484.862	24765.600	76003.600
<i>Inga edulis</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	11.907	0.224	10.090	14.555
<i>Inga edulis</i>	Leaf dry matter content	LDMC	mg/g	25	493.683	6.494	428.298	545.679
<i>Inga edulis</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.085	0.002	0.069	0.099
<i>Leucaena leucocephala</i>	Leaf area	LA	mm <sup>2</sup>	25	19356.276	651.367	12600.900	26843.200
<i>Leucaena leucocephala</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	23.042	0.519	18.780	29.670
<i>Leucaena leucocephala</i>	Leaf dry matter content	LDMC	mg/g	25	328.458	6.618	251.497	397.260
<i>Leucaena leucocephala</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.044	0.001	0.034	0.053
<i>Musa L.</i>	Leaf area	LA	mm <sup>2</sup>	25	1867132.352	73625.031	1354939.200	2772397.600
<i>Musa L.</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	27.906	0.860	15.922	34.129

Musa L.	Leaf dry matter content	LDMC	mg/g	25	231.576	7.322	190.704	347.656
Musa L.	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.037	0.002	0.029	0.063
Musa L.	Stem specific density	SSD	mg/cm <sup>3</sup>	3	0.037	0.003	0.029	0.044
Musa L.	Maxium potential height	Hmax	m	5	5.320	0.177	5.000	6.000
Mangifera indica	Leaf area	LA	mm <sup>2</sup>	25	7349.768	648.176	2561.300	18091.300
Mangifera indica	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	7.267	0.212	5.180	9.429
Mangifera indica	Leaf dry matter content	LDMC	mg/g	25	435.603	5.149	399.371	490.909
Mangifera indica	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.140	0.004	0.106	0.193
Nephelium lappaceum	Leaf area	LA	mm <sup>2</sup>	25	18166.288	1045.328	10405.500	27869.600
Nephelium lappaceum	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	8.469	0.232	6.937	10.335
Nephelium lappaceum	Leaf dry matter content	LDMC	mg/g	25	469.068	4.733	431.703	527.495
Nephelium lappaceum	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.120	0.003	0.097	0.144
Sapium glandulosum	Leaf area	LA	mm <sup>2</sup>	25	6743.296	581.191	3255.200	15041.100
Sapium glandulosum	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	11.853	0.789	7.520	20.572
Sapium glandulosum	Leaf dry matter content	LDMC	mg/g	25	347.937	18.090	193.103	478.873
Sapium glandulosum	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.092	0.005	0.049	0.133
Persea americana	Leaf area	LA	mm <sup>2</sup>	27	11136.956	1044.848	4355.300	25194.100
Persea americana	Specific leaf area	SLA	mm <sup>2</sup> /mg	27	10.832	0.322	8.268	14.142
Persea americana	Leaf dry matter content	LDMC	mg/g	27	437.608	4.152	403.141	490.323
Persea americana	Specific leaf weight	SLW	mg/mm <sup>2</sup>	27	0.094	0.003	0.071	0.121
Spondia dulcis	Leaf area	LA	mm <sup>2</sup>	30	30618.523	1193.201	20708.300	42740.400
Spondia dulcis	Specific leaf area	SLA	mm <sup>2</sup> /mg	30	23.221	1.471	12.550	43.701
Spondia dulcis	Leaf dry matter content	LDMC	mg/g	30	191.824	10.656	77.731	366.667
Spondia dulcis	Specific leaf weight	SLW	mg/mm <sup>2</sup>	30	0.048	0.003	0.023	0.080
Spondia mombin	Leaf area	LA	mm <sup>2</sup>	26	44771.169	2630.984	23415.100	69797.900
Spondia mombin	Specific leaf area	SLA	mm <sup>2</sup> /mg	26	14.024	0.507	9.703	18.903
Spondia mombin	Leaf dry matter content	LDMC	mg/g	26	320.611	6.133	278.779	392.670
Spondia mombin	Specific leaf weight	SLW	mg/mm <sup>2</sup>	26	0.074	0.003	0.053	0.103

<i>Spondias purpurea</i>	Leaf area	LA	mm <sup>2</sup>	25	9599.044	419.154	5619.700	13551.000
<i>Spondias purpurea</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	20.941	0.993	16.249	37.293
<i>Spondias purpurea</i>	Leaf dry matter content	LDMC	mg/g	25	216.138	4.405	169.811	270.718
<i>Spondias purpurea</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.050	0.002	0.027	0.062
<i>Tabebuia rosea</i>	Leaf area	LA	mm <sup>2</sup>	25	57022.800	3838.798	24262.700	111250.400
<i>Tabebuia rosea</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	8.948	0.364	6.600	12.291
<i>Tabebuia rosea</i>	Leaf dry matter content	LDMC	mg/g	25	420.155	12.020	305.908	521.120
<i>Tabebuia rosea</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.116	0.004	0.081	0.152
<i>Terminalia oblonga</i>	Leaf area	LA	mm <sup>2</sup>	25	6180.844	269.969	3708.600	8291.600
<i>Terminalia oblonga</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	12.614	0.237	10.944	15.683
<i>Terminalia oblonga</i>	Leaf dry matter content	LDMC	mg/g	25	453.591	8.557	388.350	549.550
<i>Terminalia oblonga</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.080	0.001	0.064	0.091
<i>Theobroma cacao</i>	Leaf area	LA	mm <sup>2</sup>	42	29855.014	1024.897	18096.400	46719.900
<i>Theobroma cacao</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	42	12.649	0.346	9.215	18.816
<i>Theobroma cacao</i>	Leaf dry matter content	LDMC	mg/g	42	421.298	5.845	360.054	528.967
<i>Theobroma cacao</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	42	0.081	0.002	0.053	0.109
<i>Zanthoxylum riedelianum</i>	Leaf area	LA	mm <sup>2</sup>	25	82573.476	5313.165	43485.100	145002.600
<i>Zanthoxylum riedelianum</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	25	11.449	0.221	9.794	14.741
<i>Zanthoxylum riedelianum</i>	Leaf dry matter content	LDMC	mg/g	30	386.707	12.583	249.575	503.670
<i>Zanthoxylum riedelianum</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	25	0.088	0.002	0.068	0.102
<i>Shizolobium parahyba</i>	Leaf area	LA	mm <sup>2</sup>	26	168671.550	9297.777	81069.000	257375.800
<i>Shizolobium parahyba</i>	Specific leaf area	SLA	mm <sup>2</sup> /mg	26	12.391	0.326	9.755	16.400
<i>Shizolobium parahyba</i>	Leaf dry matter content	LDMC	mg/g	26	438.700	9.722	362.912	610.788
<i>Shizolobium parahyba</i>	Specific leaf weight	SLW	mg/mm <sup>2</sup>	26	0.082	0.002	0.061	0.103