

## REVIEW

# Shade tree trait diversity and functions in agroforestry systems: A review of which traits matter

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**Handling Editor:** Akira Mori**Abstract**

1. Shade trees in agroforestry systems confer ecosystem services, such as enhanced soil fertility from diverse litter inputs, microclimate regulation via shade, and disease mitigation through trophic and abiotic interactions. With this thriving role of agroforestry in sustainable agriculture, particularly for tree crops, systematic and reliable methods to select shade trees for specific agroecosystem outcomes are crucial.
2. Plant functional traits offer a framework to describe, select and manage shade trees. Over the last decade, shade tree leaf functional traits and whole plant traits have been assessed in agroforestry systems. Yet, we lack amalgamated information on (i) what we know about shade tree trait relationships with functions to achieve desired agroecosystem outcomes, (ii) how decades of shade tree selection by farmers impacts agroforests inter- and intraspecific trait diversity, and (iii) which shade tree traits should be considered for achieving farmer priorities.
3. We consolidate literature on *Coffea arabica* (coffee) and *Theobroma cacao* (cocoa) agroforestry systems to summarize the role of shade tree functional traits in three key ecosystem functions: soil fertility, microclimate modification and crop productivity. We compile global and regional datasets on tree functional trait diversity to show the functional space of agroforestry tree species compared with the overall functional space observed in plants.
4. Despite, or maybe because of, high shade tree diversity, shade tree trait characterization remains coarse and commonly measured at the community scale in the literature. Based on published trait data, we show that farmers adjust the functional composition of shade trees to increase the recycling of soil nutrients (high leaf nitrogen), the production of wood (skewing towards lower wood densities) and the production of fruits (tendency towards high seed size). Common shade trees in coffee and cocoa systems fall in the mid-range of leaf acquisitive to

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conservative strategies, providing evidence that expanding shade tree portfolios can improve, or even accelerate, functions.

5. *Synthesis and applications*: Based on the agroforestry literature and on trait-environment relationships, we propose a matrix of shade tree traits that influence desirable agroecosystem outcomes for farmers, which can guide fine-scale coordination of trait expression and agroforestry functions.

#### KEYWORDS

agrobiodiversity, agroecosystems, *Coffea arabica* (coffee), functional space, functional traits, leaf traits, shade trees, *Theobroma cacao* (cocoa)

## 1 | INTRODUCTION: TREE CHARACTERIZATION IN AGROFORESTRY SYSTEMS

The integration of trees into agricultural landscapes, or agroforestry, addresses many of the most pressing issues of our time (Jose, 2009; Tschardt et al., 2011; Somarriba et al., 2012). Increasing biodiversity in agricultural systems is associated with improved ecosystem functions (Tamburini et al., 2020), and specifically, agroforestry practices can result in enhanced local soil fertility, reductions in greenhouse gas emissions, positive microclimate modification, and disease mitigation through various trophic and abiotic interactions (Kim & Isaac, 2022; Malézieux et al., 2009; Muchane et al., 2020).

Defining the optimal tree species to achieve specific functions in agroforestry systems, notably in shaded *Coffea arabica* (coffee) and *Theobroma cacao* (cocoa) systems, is a common theme within agroforestry research. Tree characterization in agroforestry has relied heavily on tree biology or tree diversity, such as shade tree phenology, canopy exposure or climatic envelope (Asare & Anders, 2016; Abdulai et al., 2018; Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020). Some approaches focus on reducing the number of key characteristics for tree selection, by narrowing to a singular shade tree parameter, for instance, based on tree height (e.g. Blaser-Hart et al., 2021). Other approaches use shade composition (number of shade tree species) and level (quantity of shade) as the common metrics for describing shade in agroforestry systems, with approximately half of these studies including shade tree functional type (Piato et al., 2020). Modelling has proven a popular approach to selecting optimal shade trees in both coffee and cocoa agroforestry systems. Such models tend to focus on the impacts of shade trees on alleviating water and temperature stress of crops (e.g. Rahn et al., 2018) or on light competition between species (e.g. Charbonnier et al., 2013). Locally developed and highly nuanced knowledge of shade trees underpins much of tree selection (Cerdan et al., 2012; Isaac et al., 2018; Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020). While summarizing farmers' shade tree preference information into platforms for shade tree selection has been done (see ShadeTreeAdvice platform; Rigal et al., 2022 or agroforestry switchboard; ICRAF), the output of these approaches tends to remain at the taxonomic level, suggesting specific species over specific functions.

Beyond taxonomy, plant functional traits offer a framework to describe, select and manage shade trees. Plant functional traits include any morphological, anatomical, physiological, biochemical and phenological characteristic that is measurable at the individual plant level (Kattge et al., 2020; Violle et al., 2007). The expression of these traits is determined by genetic and community assembly processes (Kraft & Ackerly, 2014) and reflects how plants adapt to biotic and abiotic constraints. Plant traits have opened new possibilities to understand ecological processes by using them as a common currency to assess plant communities from different ecosystems irrespective of their taxonomic composition (McGill et al., 2006). For instance, plant trait studies have helped to shed light on how plants (i) respond to broad environmental conditions (Moles et al., 2007; Ordoñez et al., 2009; Wright et al., 2005), (ii) are linked to other trophic levels (Loranger et al., 2012) and (iii) affect ecosystem processes (for instance nutrient cycling; Aerts & Chapin, 2000; Cornwell et al., 2008; Weedon et al., 2009), which are the basis of ecosystem services.

A growing body of literature exists on using functional traits as a way to describe and predict agroecosystem function in agricultural systems (cover crops—Blesh, 2018; Finney & Kaye, 2016; cereals and legumes—Ajal et al., 2021; Nimmo et al., 2023; vegetable crops—Rolhauser et al., 2022; and weeds—Archibald et al., 2022). And multiple papers have suggested plant functional traits as key to generalizing the selection of shade trees (Isaac & Borden, 2019; Rigal et al., 2022; Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020). Shade tree traits are increasingly used in the agroforestry literature, with over 150 papers published in the last decade on 'agroforestry' and 'functional traits'. Yet, a cumulative assessment of the agroforestry literature on which shade tree traits are measured in agroforestry systems, and more importantly, which leaf trait expression drives ecosystem functions, remains absent. As diversifying agricultural systems continues to be an essential component to achieving sustainability (Blesh et al., 2023), establishing clear trends between diversity and function remains critical to successful transitions.

Here, we conduct a review of the literature and consolidate information on shade tree traits and ecosystem function relationships, specifically in *Coffea arabica* (coffee) and *Theobroma cacao* (cocoa) agroforestry systems. From this information, we summarize what we currently know about the role of shade tree functional traits in conferring three key ecosystem functions: soil fertility, microclimate

modification and crop productivity. We then use global and regional datasets on tree functional trait values to show how shade tree selection by farmers (in four of the most common agroforestry systems in Central America) impacts the overall trait space compared with plants in general, and how functional trait trade-offs may influence optimal agroforest functioning. Finally, we propose a matrix of shade tree traits that influence desirable agroecosystem outcomes for farmers to fine-tune the functional reasoning behind agroforestry design and inform recommendations that are promoted by various stakeholders.

## 2 | WHAT WE KNOW—FUNCTIONAL TRAITS AND ECOSYSTEM FUNCTION

Plant traits are related to different ecosystem processes and properties, but also as syndromes of trait covariation. These syndromes describe important trade-offs in plant functioning as a continuum (Westoby et al., 2002). Three of the most studied examples show how plants balance: growth versus conservation of resources (leaf economics spectrum, including specific leaf area [SLA], leaf dry matter content, leaf nitrogen [LNC]; Reich et al., 1997; Wright et al., 2004); seed size vs their capacity to colonize, compete and persist (life history spectrum; Falster & Westoby, 2005; Moles & Leishman, 2008); and wood density versus water conductive efficiency and mechanical strength (Chave et al., 2009; Westoby & Wright, 2006). Other syndromes involving other traits, such as plant roots, likely exist but have been less studied.

Plant traits are generally measured at the individual level, but can be upscaled to species within communities, and to the whole plant community level. Commonly, studies of plant trait effects on ecosystem processes are carried out with aggregated trait values of plant communities, since plant-mediated impacts will depend on the combined effects of the traits of all species that compose a given community (Funk et al., 2017; Lavoura & Garnier, 2002). To account for differences in the dominance of species, species trait values are weighted by the contribution of the species to the total biomass of the community (community-weighted means, CWM). Thus, the trait values of the most dominant contributors will drive the trait value of the community and the instantaneous functioning of ecosystems (Garnier et al., 2004; Grime, 1998). Ideally, community means should be weighted by dominance (considering biomass or basal area in the case of woody species), but approximations using abundance are also accepted in the absence of biomass data (Funk et al., 2017; Lavelle et al., 2008).

Instead, functional diversity indicators characterize the inter-specific variability in trait values within a community. Functional diversity has been used mainly to understand the mechanisms underpinning the relationship between diversity and ecosystem functions (Gross et al., 2017; Mason et al., 2005), and community assembly and niche partitioning (Cornwell & Ackerly, 2009; Kraft & Ackerly, 2014; Kraft et al., 2008). Approaches assessing functional diversity have been designed similarly to the methods to quantify

taxonomic diversity, for instance by estimation of alpha and beta trait diversity (Ackerly & Cornwell, 2007), by assessment of functional groups (Petchey & Gaston, 2006) or by various diversity indexes that summarize the richness, evenness and divergence within a community as a continuous index (Mason et al., 2005).

These functional trait-based approaches have made significant contributions to understanding the effects of trait expression on ecosystem function. Over the last decade, this approach has been applied to assess the impact of shade tree selection on ecosystem processes and to define a repeatable method to establish widely applicable recommendations for suitable shade trees in diverse agroecosystems. To date, an array of studies have made these links, specifically in shade-grown coffee and cocoa agroforestry systems, where a large pool of shade species is accommodated by farmers in smaller assemblages within production plots. Within these plots, the functional characteristics of species affect various ecosystem processes. Here, we provide evidence of the main relationships between shade tree characteristics, including whole plant and leaf functional traits and three dominant functions in agroforestry systems: soil fertility, microclimate modification and crop performance.

### 2.1 | Shade tree traits and impacts on soil fertility

Numerous studies on the benefits of agroforestry on soil fertility exist (Albrecht & Kandji, 2003; Beillouin et al., 2021; Dollinger & Jose, 2018; Lal, 2004; Tschantke et al., 2011). Studies on soil fertility in cocoa and coffee agroforestry systems commonly highlight null to positive impacts on soil carbon (C) and soil fertility (Getachew et al., 2023; Isaac et al., 2007; Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020; Wartenberg et al., 2020), as well as on soil biodiversity (Muleta et al., 2007; Sauvadet et al., 2019; Sewnet & Tuju, 2013) under shade tree canopies. Over the last decade, data have emerged on the impacts of specific shade tree traits on soil functions. When measured, litter traits such as N, phosphorus (P) and calcium (Ca) content have been shown to have direct impacts on soil properties in coffee and cocoa agroforestry systems (Isaac et al., 2007; Sauvadet et al., 2019; Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020; Wartenberg et al., 2020). Specific litter traits have also been linked to soil biodiversity under shade tree canopies (Moço et al., 2010), where enhanced soil fertility is, broadly, associated with shade tree leaf litter decomposability, thus influencing soil biological activity. However, this influence may vary with management intensity in agroforestry systems (Sauvadet et al., 2019) and is mostly observed directly under shade tree canopies (e.g. Blaser et al., 2017).

Instead, the impacts of shade tree presence on soil fertility exhibit less marked trends when studied at the plot scale, and often find low to no impacts of agroforestry systems compared with monoculture on soil properties (Abou Rajab et al., 2016; Romero-Alvarado et al., 2002; Siles et al., 2010). Indeed, a tree's impacts on soil fertility present a high spatial heterogeneity, with decreasing influence with the distance to their trunk (Cardinael et al., 2019; Guillot et al., 2021). The spatialization of a tree's influence on soil fertility, unfortunately

often overlooked (Cardinael et al., 2017), has also been shown in cocoa agroforestry systems by Blaser et al. (2017) and Wartenberg et al. (2020); localized benefits of shade trees were not detectable at the plot scale or away from shade tree canopies. Nonetheless, several studies at the plot scale did find significant soil fertility enhancement in agroforestry systems, such as Méndez et al. (2009) who observed that soil fertility increased with shade tree species richness within agroforests, while Rousseau et al. (2021) found that soil macrofauna was rather responding to the density of specific tree species with the community. Furthermore, Häger and Avalos (2017) found that soil organic C increased with higher CWM wood density and with higher variability in tree maximal height across the systems studied. Such analyses could be extended to a wider range of functions including survivorship or of other traits by leaning on the global TRY database, as Wallwork et al. (2022) did to link naturally regenerating tropical forest traits with increases in soil organic C. Wallwork et al. (2022) were thus able to find strong relationships between CWM traits with soil C, which were of the same nature with those found with localized shade tree impacts—that is, positive relationships between soil C, leaf N content and SLA.

These contrasting trends suggest that while shade tree benefits in soil fertility may be harder to detect at the plot scale than under their canopies, this objective may still be achievable by increasing trait characterization at the shade tree community scale. Indeed, studies comparing soil properties at the plot scale generally lean on a coarse characterization of shade tree community traits, mostly related to light transmission regulation (such as canopy cover) or C storage in tree biomass (deduced from allometric equations based on tree height and DBH for instance; Abou Rajab et al., 2016; Romero-Alvarado et al., 2002; Siles et al., 2010), which may not always be fine-scale enough to understand the presence or absence of shade tree benefits on soil fertility. Refining shade tree community characterization, and testing more contrasting community compositions, may help improve our understanding of shade tree impacts on soil fertility at the plot scale.

## 2.2 | Shade tree traits and impacts on microclimate modification

One of the principal objectives of agroforestry is the capacity to modify microclimate at various scales. We know that coffee and cocoa agroforestry systems moderate air temperatures and relative humidity (Vaast et al., 2008), increase soil moisture (Lin, 2007), reduce irradiance levels (Charbonnier et al., 2017) and change throughfall characteristics (Siles et al., 2010), leaf wetness dynamics (López-Bravo et al., 2012) and wind speed (Cleugh, 1998). Much of this knowledge comes from analyses of specific tree species and their leaf traits within agroforestry systems (most commonly SLA and LNC; van Oijen et al., 2010).

More commonly reported in the literature is the role of tree canopies in microclimate modifications, namely canopy geometry and canopy foliage density. Yet, it is clear from the literature that traits

at the canopy and leaf-level work in tandem. For instance, leaf traits, such as thicker leaves, reduce wind speeds together with canopy characteristics (Gagliardi et al., 2020), likely because they are more resistant to reconfiguration in strong winds (Vogel, 1989), and so are better able to maintain their windbreak effect. The slowing of wind speeds has important implications for various agroecosystem processes, including microclimate modifications, but also maintaining soil integrity to prevent soil erosion processes (Meylan et al., 2017) and preventing pests and disease diffusion (Avelino et al., 2023). At the edge of agroforests, shade trees can control the spread of airborne pests and diseases (e.g. fungal coffee pathogen *Hemileia vastatrix*; Gagliardi et al., 2020), and prevent agrochemical drift (an important consideration for neighbouring organic parcels). To confer these effects, trees at the edge of agroforests require adequate canopy height, density and numerous thick leaves with particle-capturing capacities (Avelino et al., 2023). Small-shaped leaves, such as needles, can capture airborne particles more efficiently due to their increased surface areas and contact probability with airborne particles (Jin et al., 2021). Other leaf traits that can augment particle capture include rough, wrinkled, ridged, furrowed, hairy and waxy leaves (Chiam et al., 2019; Corada et al., 2021; Dzierżanowski et al., 2011), while smooth leaves can indirectly capture airborne particles via water droplets that tend to adhere to their surfaces (Barthlott & Neinhuis, 1997).

Similarly, rainfall dynamics are largely shaped by the presence or absence of tree canopies, yet within treed systems, specific canopy and leaf-level traits together play a distinguishing role. Throughfall kinetic energy (TKE), though consistently greater beneath tree canopies than in open stands, is lower under canopies with greater leaf area index (LAI) values (likely due to enhanced redistribution of rainfall and re-interception and splitting of raindrops in multi-layered canopies), and under canopies with shorter canopy base heights (likely due to raindrops not reaching their terminal velocity; Geißler et al., 2013; Gómez et al., 2001; Liu et al., 2018). Total throughfall amounts are also reduced beneath canopies of greater LAI, likely due to the greater storage capacity of such canopies (Liu et al., 2018). Simultaneously, leaf traits, such as greater leaf area and specific leaf shapes, can reduce throughfall amounts and increase TKE through greater raindrop pooling that results in either greater canopy storage or greater leaf drip size (e.g. Nanko et al., 2006; Zhang et al., 2021). These interactions with rainfall dynamics have larger implications, as high TKE can promote splash erosion of bare soils (Geißler et al., 2013) and pathogen dispersal from infected surfaces, while reduced throughfall amounts can lead to poor wash-off of diseased surfaces (Avelino et al., 2023) and exacerbate water stress conditions (Vaast et al., 2016).

Considering air temperature and relative humidity, research has demonstrated that taller trees with lower canopy base heights, larger leaves and dense, homogenous canopies can better moderate air temperature extremes and increase relative humidity (e.g. Blaser-Hart et al., 2021; Gagliardi et al., 2021; Merle et al., 2022). This is likely due to such trees more effectively isolating layers of air beneath their canopies, preventing moisture loss and excessive air

mass heating (Merle et al., 2022). These changes can have both positive (e.g. enhanced microclimates for crops, which can extend optimal growth regions; Beer, 1987) and negative effects on perennial crops in the understory (e.g. modifying pest and disease dynamics; Avelino et al., 2023). The detailed nuances between shade tree trait expression have important implications for the suitability of certain species for distinct functions, as well as the potential for such details to inform tree management regimes (i.e. pruning practices).

### 2.3 | Shade tree traits and their impacts on crop productivity

Coffee and cocoa are widely considered as shade-tolerant species, which express strong plastic responses to environmental variability (Chaves et al., 2008; DaMatta, 2004; Jaramillo-Botero et al., 2010; Rodríguez-López et al., 2014) that may influence reproductive output (Gagliardi et al., 2015; Martin & Isaac, 2021). While much has been explored regarding leaf traits of sun leaves and shade leaves of individual coffee and cocoa plants and impacts on yield (DaMatta, 2004), we have a coarser understanding of the interactions between shade tree species composition and yield. These interactions are predominantly related to light regulation, and subsequently photosynthesis rates, where yield is highly correlated with the incident light received, but not necessarily linearly, rather with an optimal shade level. This relationship between shading and coffee and cocoa productivity depends on shading intensity, but also crop age and cultivar, and spatial/environmental conditions (e.g. Asare et al., 2019; Niether et al., 2020). Among ~30 studies on robusta coffee agroforestry, Piato et al. (2020) showed clear relationships between shade and yield, highlighting that older agroforests exhibit higher coffee growth and productivity with shade, with inverse effects in younger agroforests. In many cases, agroforestry systems tend to decrease crop raw productivity when light interception per shade tree is high (e.g. Ramírez-Argueta et al., 2022), as evidenced by the positive relationship between cocoa plant individual yield and their distance to shade trees, found in Koko et al. (2013) and da Silva Neto et al. (2018).

It is notable though that in each of these studies relating shade tree taxa to productivity, shade tree characterization stops short of describing traits linked with function, rather studies rely on descriptions such as height and canopy cover. While these characteristics are important, they reflect plant ecophysiological processes occurring at the leaf level, for instance, the LAI, which is important for canopy scale processes, such as photosynthesis and precipitation interception, can be calculated from the key leaf functional trait SLA (Fang et al., 2019).

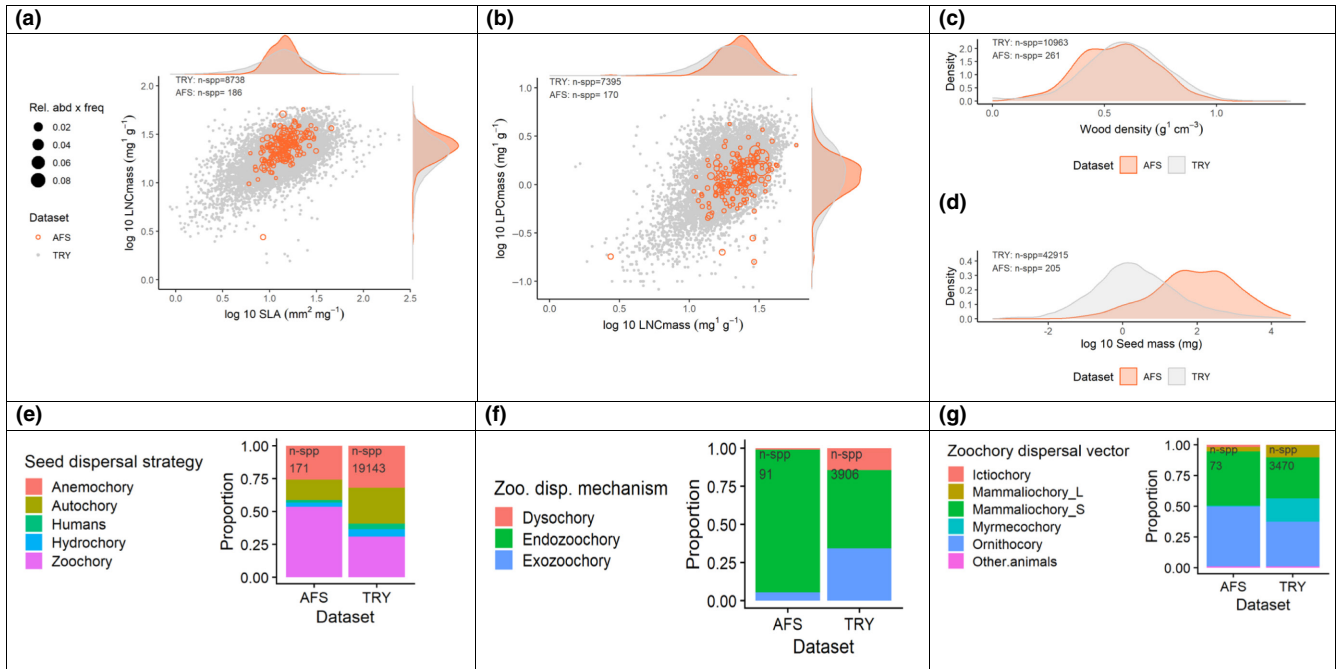
Nonetheless, many studies also find higher yields in agroforestry systems compared with monocultures (e.g. Asare et al., 2019). For instance, Asitoakor et al. (2022) reported higher cocoa yield under the shade of four out of eight candidate species in Ghana, suggesting this is due to shade tree morphological structure (open canopies that promote aeration and light penetration and enhance photosynthesis,

flowering, fruiting and crop production). Yet, such higher yields in agroforestry compared with monocultures may be due to other functions provided by shade trees, such as microclimate regulation (e.g. Niether et al., 2018), especially facing extreme climatic events, pest regulation (Daghela Bisseleua et al., 2013; Djuideu et al., 2021) and soil fertility enhancement (e.g. Sauvadet, Asare, et al., 2020; Sauvadet, Saj, et al., 2020). Shade tree traits related to these functions also ensure yield, depending on local environmental constraints (e.g. Hagggar et al., 2011; Sauvadet et al., 2019). Agroforestry systems may even provide higher yield than monocultures when fruit species are used as shade trees, given the additional contribution of food and other goods (Armengot et al., 2016; Niether et al., 2020), and thus should also be taken into account in shade tree trait selection.

## 3 | WHAT TRAIT SPACE IS AVAILABLE FOR FARMERS? FUNCTIONAL TRAIT DIVERSITY IN AGROFORESTS

To illustrate the functional space of shade species in agroforestry systems, we compared the functional diversity of agroforestry systems in Central America (shaded coffee, cocoa, silvopastures and live fences,  $n$  plots=2517) versus the overall functional diversity of plants globally, using the TRY database (Kattge et al., 2020), as detailed in Supporting Information. The four main agroforestry systems in Central America harbour across the region ~460 shade species that include trees, shrubs, palms, and other species such as large monocots and herbs (Esquivel et al., 2023). These agroforestry plots have a median of ~23 shade species  $\text{ha}^{-1}$  (range 1–800), but with a high species turnover between plots and regions. If we assess the gamma functional space by selecting the most abundant species (that account for >80% of species abundance within plots), the pool of the most abundant species in these Central American agroforestry systems corresponds to 338 species that include mainly trees, but also other growth forms. When these agroforestry taxa are compared with the overall functional diversity of plants (as recorded in the global TRY database (Kattge et al., 2020); see Supporting Information), we show that farmers adjust the functional composition of the shade component to increase:

1. the recycling of nutrients in the soil (Figure 1a,b)—particularly for LNC, with SLA and leaf phosphorus content (LPC) values as intermediate. Of the 10 agroforestry species with the highest LNC, eight correspond to legumes species, whose LNC ranged between 38.7 and 50.8  $\text{mg g}^{-1}$ , and included *Albizia guachapele*, *Albizia niopoides*, *Chloroleucon mangense*, *Erythrina poeppigiana*, *Inga sapindoides*, *Inga vera*, *Leucaena leucocephala*, *Senegalia polyphylla* and *Vachellia collinsii*.
2. the production of wood (Figure 1c)—farmers seem to favour, particularly fast-growing and easy-to-work species. We show a slight skewing towards low to intermediate wood densities and
3. the production of food (edible fruits) (Figure 1d)—the active selection of trees and palms with edible fruits with large seeds is shown



**FIGURE 1** Comparison of the functional trait distribution of the most common species that are present in 2015 plots across four agroforestry systems in Central America, versus the overall distribution of all plant species for which information is available in the TRY database, along with important axes of plant specialization. Panels (a and b) show the bivariate distribution of different combinations of leaf traits that are related to the leaf economics spectrum. The size of the symbols corresponds to the relative frequency  $\times$  relative plot abundance of shade species across 2517 plots. Species with high values represent species that are abundant in a plot and occur in a high number of plots. Panels (c and d) show the univariate distribution of wood density (c) and seed mass (d). Panels (e–g) represent the proportional prevalence of seed dispersal strategies: (e) For overall seed dispersal strategies, (f) The mechanisms of animal seed dispersal and (g) The vector of animal seed dispersal. Comparisons are made using species means. The number of observations for each comparison varies following data availability. For a full explanation of methods, see [Supporting Information](#).

by the higher average seed mass (969.1 mg per seed), and a clear tendency in the trait distribution towards high seed size in trees selected for agroforestry systems. Out of 10 agroforestry species with the heaviest seeds, eight correspond to edible fruits such as *Acrocomia aculeata*, *Artocarpus altilis*, *Casimiroa tetrameria*, *Juglans regia*, *Mammea americana*, *Mangifera indica*, *Persea americana* and *Pouteria sapota*.

Many of the most common species across these four agroforestry systems fit these objectives. For instance, within the 10 most common shade species across all systems (see methods in Supporting Information), there are two legume species (*Gliricidia sepium* and *Inga vera*), four timber species (*Cedrela odorata*, *Cordia alliodora*, *Pachira quinata* and *Swietenia macrophylla*), and one fruit species (*Persea americana*). All these species have relatively high values of LNC in plants ( $17\text{--}39\text{ mg g}^{-1}$ ) and wood with intermediate densities ( $0.41\text{--}0.59\text{ g cm}^{-3}$ ), ideal for producing timber products. The active selection of fruit trees reinforces natural processes of seed dispersal in tropical forests, where zoochory is one of the main mechanisms (Correa et al., 2023). Although the conservation of fauna is not an objective per se for farmers, by favouring the production of fruit trees in agroforestry systems, they inadvertently create suitable habitats and biological corridors for wild fauna (Estrada-Carmona et al., 2019; Harvey et al., 2008).

Moreover, it is clear from this analysis that there is a wide space where natural processes have a great influence on the species that make up the shade component of agroforestry systems. On the one hand, within the 10 most common species, there were two fast-growing and highly proliferating species, *Bursera simaruba* and *Guazuma ulmifolia* ( $18\text{--}30\text{ mg g}^{-1}$  LNC), low to intermediate wood densities ( $0.35\text{--}0.52\text{ g cm}^{-3}$ ), and light seeds ( $4.3\text{--}110.3\text{ mg}$  per seed) dispersed by birds and small mammals. Although they do not offer a direct benefit to farmers in terms of food production, they do offer benefits such as shade or biomass production for firewood. These species are not actively planted by farmers (Ordonez et al., 2014), but their functional profile coincides with tree characteristics that farmers look for in a shade tree species (Cerdan et al., 2012), through both observation and advice (Isaac et al., 2021). On the other hand, it seems that there are also remnants of natural forest species characterized by more conservative functional strategies (Lohbeck et al., 2012). Although very low values of SLA, leaf nutrient contents or wood density (reflective of conservation and persistence strategies) are not observed for the most common species found in agroforestry systems, these species can cover a large spectrum of trait values for these three traits (Figure 1a,b), increasing the overall functional diversity of agroforestry systems.

While there is large functional space through interspecific trait variation, there is also considerable intraspecific variation (ITV) that

is important for different reasons. Many studies warn about the importance of ITV in understanding the relationships between plant community assembly and ecosystem functioning (Shingley et al., 2016; Siefert et al., 2015; Westerband et al., 2021). Indeed, while ITV remains hard to predict since its amplitude varies widely between species, traits and environmental conditions, its general extent makes its consideration essential in trait-based decision frameworks (Martin & Isaac, 2015). It is well known that environmental conditions, such as light incidence (Buchanan et al., 2019; Miyaji et al., 1997), water availability (Acheampong et al., 2015; Carminati & Javaux, 2020; Tezara et al., 2020) or soil fertility (Borden, Anglaaere, et al., 2020; Borden, Thomas, et al., 2020; Maire et al., 2015) will impact both shade trees' and perennial crops' ITV. These variations are often expressed relative to changes in resource acquisition strategy (Blasini et al., 2021; Westerband et al., 2021), based on the concept of the LES—and later the Plant Economic Spectrum—the same principle as the LES but including stem and root traits and their importance for water, C and nutrient acquisition strategies (Reich, 2014).

As a consequence, shifts in resource acquisition strategies lead to changes in different sets of traits, widely observed at several levels—phenotypic plasticity, genetic correlation, population-local adaptation—and factors, including adaptations to environmental constraints (Agrawal, 2020). For instance, increased shading will induce more investment from the plants for light acquisition, by increasing their SLA to improve their light acquisition potential, but also their leaves' N content (Gagliardi et al., 2015) to build more photosynthesis-related enzymes such as Rubisco (Ávila-Lovera et al., 2016), leading to frequent coordination between these traits (e.g. Shingley et al., 2005). Knowing such common trait syndromes can reduce the number of traits required to select appropriate tree species, yet it should be taken cautiously, as the traits and organs' sensitivity to ITV varies. Indeed, the global meta-analyses of Siefert et al. (2015), and Westerband et al. (2021), highlight greater ITV extent for whole plant traits than organ-specific traits, but also higher leaf chemical ITV than morphological ITV. These differences in

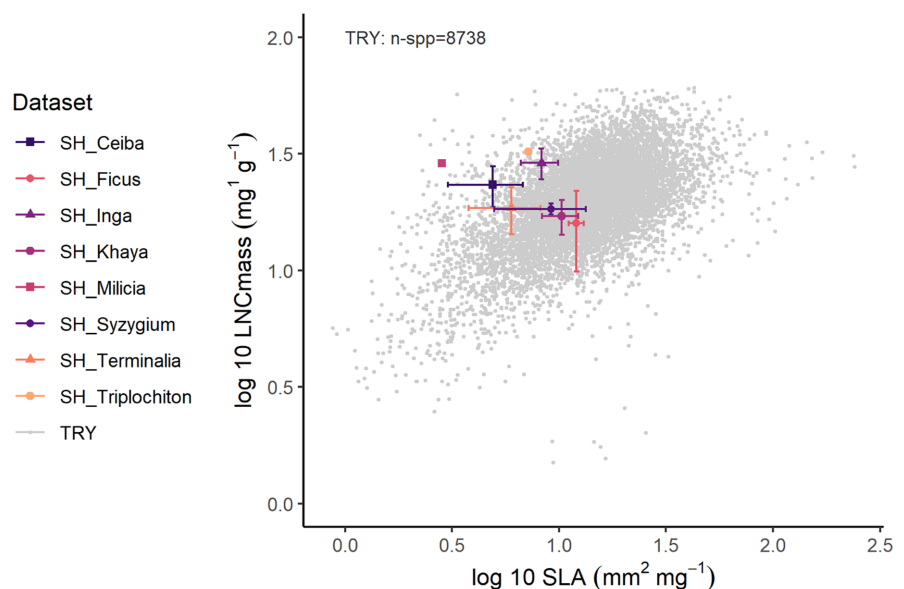
amplitude were attributed to varying degrees of phenotypic plasticity and genetic regulation.

To illustrate shade tree ITV, Figure 2 depicts the mean and standard deviation of SLA and LNC from the TRY database (Kattge et al., 2020) of eight common shade tree genera derived from [www.shadetreeadvice.org](http://www.shadetreeadvice.org). The range of trait expression within a genus is variable but large. For instance, individuals in the genus *Ficus* express very high plasticity in LNC but restricted plasticity in SLA. Timber genera, *Terminalia*, *Ceiba* and *Khaya* express a nearly equal range of plasticity for both traits. What is also clear is a systematic and expected trait trade-off between LNC and SLA. This trade-off is well documented among species (Wright et al., 2004) and within species (Martin et al., 2017). This reliance on trait trade-offs provides an opportunity to reduce the trait dimensionality for shade trees. For instance, we know that higher LNC is typically correlated with higher SLA, confirming trait syndromes. These syndromes can be used by farm managers to focus on one or two key traits that predictably covary with other traits.

#### 4 | SHADE TREE TRAITS FOR ACHIEVING FARMER PRIORITIES

The application of traits and trait research in agroforestry systems represents an important opportunity to further inform agroforestry design and on-farm practices. Based on our review of evidence and data consolidation from the literature, we summarize key functions and services and their association with specific leaf and whole plant shade tree traits (Table 1). When farmers select shade trees, they can prioritize a specific service or multiple services from a basket of options that can be traced back to associated functions and shade tree traits that achieve those functions. The selection of trees based on specific traits can enhance certain functions more accurately than taxa-based selection alone. These links between traits and functions are moderated by specific

**FIGURE 2** Leaf nitrogen (LNC mass  $\text{mg}^{-1}$ ) to specific leaf area (SLA  $\text{mm}^2 \text{mg}^{-1}$ ) with 8738 species data from the TRY database and 8 of the most common shade tree genera for coffee and cocoa agroforestry (determined with shade tree advice platform) with their confidence limits, derived from the TRY database. These two functional traits are key indicators for rates of nutrient cycling and soil nutrient availability and location on the trade-off axis indicates conservative to acquisitive leaf strategies.



**TABLE 1** Shade tree traits (leaves, canopy and trunk) are commonly characterized in cocoa and coffee agroforestry systems with their level of plasticity. Also shown are trait-associated functions with directionality (+/-), associated services and the mechanisms to achieve these functions and services.

Organ	Traits	Plasticity	Associated function	Associated service	Mechanisms
Leaves	Leaf N	High	Litter decomposition (+)	Soil fertility Carbon storage	High litter turnover will allow fast nutrient cycling
	Leaf C:N	High	Litter decomposition (-)	Soil fertility Carbon storage	Low litter turnover will slow down nutrient cycling but increase soil C
	Thickness	High	Windbreak (+)	Microclimate moderation	Resistance against wind moderates airflow
	Leaf area	High	Particle capture (-) Throughfall (-) TKE (+)	Microclimate moderation Pest and disease regulation	Particle adherence and water pooling on leaf surfaces change rainfall dynamics and influence pests and disease
Canopy	SLA	High	Litter decomposition (+)	Soil fertility Carbon storage	High litter turnover will allow fast nutrient cycling
	Leaf texture	Low	Light interception (+)	Microclimate moderation	A buffered microclimate is favourable for litter decomposition throughout the year
	Litter lignin & phenols	Low	Particle capture (+) Litter decomposition (-)	Pest and disease regulation Soil water cycling	Particle adherence to leaf surfaces influences pests and disease Low litter turnover favours the presence of permanent soil mulching
Trunk	Density	-	Light interception (-) Windbreak (+)	Microclimate moderation Pest and disease regulation	Lower light transmission and airflow modulate humidity and influence pests and disease
	Openness	-	Light interception (+) Throughfall (+) TKE (+)	Microclimate moderation Pest and disease regulation	Higher light transmission and airflow modulate humidity and influence pests and disease
	Height/area	-	Light interception (-) Windbreak (+)	Microclimate moderation Pest and disease regulation	Higher light transmission and airflow modulate humidity and influence pests and disease
	Fruit production	-	-	Provisions	Fruit production for consumption or sale
Trunk	DBH/basal area & height	High	Above-ground biomass production (+)	Carbon storage	Fixation of atmospheric C within tree biomass for several decades
	Wood density	Low	Drought resistance (+)	Survival	Physiological strategy



management practices and the degree of trait plasticity. For instance, litter decomposition, a key function that strongly influences nutrient cycling and the directionality of soil C storage, is controlled by a suite of leaf traits (such as LNC, leaf lignin content and SLA) with high plasticity. Farmers can select shade trees that express a certain range of traits to achieve specific outcomes.

Given the dynamic nature of agroforests, there is a level of fluidity in desirable traits, spatially and temporally, that must be considered during agroforest design and re-design (i.e. species selection and spatial planting arrangements), and when determining best tree management practices (i.e. timing and extent of pruning practices). For instance, in regions or seasons where temperature and humidity moderation are vital for perennial crop health, such as when planting crops outside of their optimal climate range, tall, dense, homogeneous canopies with large leaves are better suited to creating optimal microclimate conditions (Avelino et al., 2023). However, shade tree canopies expressing such leaf traits could also enhance the erosive ability of rainfall and the potential short-distance dispersal of pathogens via rain, and exaggerate humidity levels in the understorey, thus making shade trees with more open canopies and small leaves better suited in regions or seasons where these concerns are a priority.

We show that farmers tend to adjust the functional composition of shade trees to increase the recycling of soil nutrients (high leaf N), the production of wood (skewing towards lower wood densities) and the production of fruits (tendency towards high seed size; Figure 1). Furthermore, common shade trees in cocoa and coffee systems fall in the mid-range of acquisitive to conservative strategies (Figure 2), providing evidence that expanding shade tree portfolios can improve or accelerate functions. While recommendations for shade tree selection are well developed, agriculture extension agencies, sustainability programmes, practitioners and researchers can benefit from a theory-based and evidence-supported shade tree taxa selection for agroforestry systems that rely on functional traits.

## 5 | AN AGENDA FOR FUTURE RESEARCH

There are a few key areas of departure between the use of functional traits in agroforestry systems and functional traits in natural systems. First, disease management commonly used in agroforestry systems, but not active in natural systems, shapes trait expression (Gagliardi et al., 2023). Given that trait handbooks (Pérez-Harguindeguy et al., 2013) recommend avoiding diseased leaves for assessments of functional traits, this creates an entirely unexplored aspect of trait trade-offs and trait space, but an overwhelmingly critical aspect of agroecosystems as the role of pest and disease management is essential. Second, following this, trait handbooks designed for natural systems may not be completely transferrable to agroecosystems. For instance, along with disease management, pruning is an essential practice in agroforestry systems, with undoubted impacts on plant growth and trait expression. Trait collections in agroforestry systems must account for the effects of pruning on all organs, leaves, canopy and trunk, of shade trees. Third, plant trait plasticity and

genetic by environment interactions in agricultural systems are critical in shaping crop functional traits (Rolhauser et al., 2022), crop trait space (Sauvadet et al., 2021), and the role of ontogeny in crop trait trade-offs and reproductive onset (Martin & Isaac, 2021). Further work is needed on shade tree genetics and ontogeny for a complete understanding of shade tree traits in ecosystem functions. Finally, as described above, the number of trait measurements needed to understand trait impacts in agroforestry may very well vary from natural systems. Given that tree introduction to a farm is predominantly through species selection and planting, filtering is already occurring, and therefore, key trait indicators for a subset of candidate species may be all that is needed to accurately assess shade tree function. Therefore, updating trait collection handbooks is required to account for practices in agroforestry systems to retrofit protocols for managed systems, and to guide fine-scale coordination of traits and agroecosystem functions.

Functional traits offer a framework to describe and select shade trees beyond taxonomy, but it is hard for farmers to make an explicit selection of species based on characteristics that are difficult to observe, such as leaf chemistry. We suggest that enhancing the quality of shade tree trait analyses and combining functional trait approaches with local knowledge to establish co-learning approaches between functional ecologists and farmers are necessary to define the most desirable shade tree characteristics and to inform the best strategies to optimize desired functions within their fields.

### AUTHOR CONTRIBUTIONS

Marney E. Isaac, Stephanie Gagliardi, Jenny C. Ordoñez and Marie Sauvadet conceived the ideas. Marney E. Isaac and Jenny C. Ordoñez consolidated and analysed the data. All authors led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

Marney E. Isaac is an associate editor of the *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

### DATA AVAILABILITY STATEMENT

Trait data from the TRY database are archived and curated at <http://www.try-db.org>.

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## REFERENCES

- Abdulai, I., Jassogne, L., Graefe, S., Asare, R., Van Asten, P., Läderach, P., & Vaast, P. (2018). Characterization of cocoa production, income diversification and shade tree management along a climate gradient in Ghana. *PLoS One*, 13, e0195777.
- Abou Rajab, Y., Leuschner, C., Barus, H., Tjoa, A., & Hertel, D. (2016). Cocoa cultivation under diverse shade tree cover allows high carbon storage and sequestration without yield losses. *PLoS One*, 11, e0149949. <https://doi.org/10.1371/journal.pone.0149949>
- Acheampong, K., Hadley, P., Daymond, A. J., & Adu-Yeboah, P. (2015). The influence of shade and organic fertilizer treatments on the physiology and establishment of *Theobroma cacao* clones. *American Journal of Experimental Agriculture*, 6(6), 347–360. <https://doi.org/10.9734/AJEA/2015/15206>
- Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, 10(2), 135–145. <https://doi.org/10.1111/j.1461-0248.2006.01006.x>
- Aerts, R., & Chapin, F. S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research*, 30, 1–67. [https://doi.org/10.1016/S0065-2504\(08\)60016-1](https://doi.org/10.1016/S0065-2504(08)60016-1)
- Agrawal, A. A. (2020). A scale-dependent framework for trade-offs, syndromes, and specialization in organismal biology. *Ecology*, 101(2), 1–24. <https://doi.org/10.1002/ecy.2924>
- Ajal, J., Jäck, O., Vico, G., & Weih, M. (2021). Functional trait space in cereals and legumes grown in pure and mixed cultures is influenced more by cultivar identity than crop mixing. *Perspectives in Plant Ecology, Evolution and Systematics*, 50, 125612. <https://doi.org/10.1016/j.ppees.2021.125612>
- Albrecht, A., & Kandji, S. T. (2003). Carbon sequestration in tropical agroforestry systems. *Agriculture, Ecosystems & Environment*, 99(1), 15–27. [https://doi.org/10.1016/S0167-8809\(03\)00138-5](https://doi.org/10.1016/S0167-8809(03)00138-5)
- Archibald, S., Alline, C., Cerdan, C. R., & Isaac, M. E. (2022). From the ground up: Patterns and perceptions of herbaceous community diversity in organic agroecosystems. *Ecological Solutions and Evidence*, 3(3), e12166.
- Armengot, L., Barbieri, P., Andres, C., Milz, J., & Schneider, M. (2016). Cocoa agroforestry systems have higher return on labor compared to full-sun monocultures. *Agronomy for Sustainable Development*, 36, 70. <https://doi.org/10.1007/s13593-016-0406-6>
- Asare, R., & Anders, R. (2016). Tree diversity and canopy cover in cocoa systems in Ghana. *New Forests*, 47, 287–302.
- Asare, R., Markussen, B., Asare, R. A., Anim-Kwapong, G., & Ræbild, A. (2019). On-farm cocoa yields increase with canopy cover of shade trees in two agro-ecological zones in Ghana. *Climate and Development*, 11, 435–445. <https://doi.org/10.1080/17565529>
- Asitoakor, B. K., Asare, R., Ræbild, A., Ravn, H. P., Eziah, V. Y., Owusu, K., Mensah, E. O., & Vaast, P. (2022). Influences of climate variability on cocoa health and productivity in agroforestry systems in Ghana. *Agriculture and Forest Meteorology*, 327, 109199.
- Avelino, J., Gagliardi, S., Perfecto, I., Isaac, M. E., Liebig, T., Vandermeer, J., Merle, I., Hajian-Forooshani, Z., & Motisi, N. (2023). Tree effects on coffee leaf rust at field and landscape scales. *Plant Disease*, 107(2), 247–261. <https://doi.org/10.1094/PDIS-08-21-1804-FE>
- Ávila-Lovera, E., Coronel, I., Jaimez, R., Urich, R., Pereyra, G., Araque, O., Chacón, I., & Tezara, W. (2016). Ecophysiological traits of adult trees of criollo cocoa cultivars (*Theobroma cacao* L.) from a germplasm bank in Venezuela. *Experimental Agriculture*, 52(1), 137–153. <https://doi.org/10.1017/S0014479714000593>
- Barthlott, W., & Neinhuis, C. (1997). Purity of the sacred lotus, or escape from contamination in biological surfaces. *Planta*, 202(1), 1–8. <https://doi.org/10.1007/s004250050096>
- Beer, J. (1987). Advantages, disadvantages and desirable characteristics of shade trees for coffee, cacao and tea. *Agroforestry Systems*, 5(1), 3–13. <https://doi.org/10.1007/BF00046410>
- Beillouin, D., Ben-Ari, T., Malézieux, E., Seufert, V., & Makowski, D. (2021). Positive but variable effects of crop diversification on biodiversity and ecosystem services. *Global Change Biology*, 27(19), 4697–4710. <https://doi.org/10.1111/gcb.15747>
- Blaser, W. J., Oppong, J., Yeboah, E., & Six, J. (2017). Shade trees have limited benefits for soil fertility in cocoa agroforests. *Agriculture, Ecosystems & Environment*, 243, 83–91. <https://doi.org/10.1016/j.agee.2017.04.007>
- Blaser-Hart, W. J., Hart, S. P., Oppong, J., Kyereh, D., Yeboah, E., & Six, J. (2021). The effectiveness of cocoa agroforests depends on shade-tree canopy height. *Agriculture, Ecosystems and Environment*, 322, 107676. <https://doi.org/10.1016/j.agee.2021.107676>
- Blasini, D. E., Koepke, D. F., Grady, K. C., Allan, G. J., Gehring, C. A., Whitham, T. G., Cushman, S. A., & Hultine, K. R. (2021). Adaptive trait syndromes along multiple economic spectra define cold and warm adapted ecotypes in a widely distributed foundation tree species. *Journal of Ecology*, 109(3), 1298–1318. <https://doi.org/10.1111/1365-2745.13557>
- Blesh, J. (2018). Functional traits in cover crop mixtures: Biological nitrogen fixation and multifunctionality. *Journal of Applied Ecology*, 55(1), 38–48. <https://doi.org/10.1111/1365-2664.13011>
- Blesh, J., Mehrabi, Z., Wittman, H., Bezner Kerr, R., James, D., Madsen, S., Smith, O. M., Snapp, S., Stratton, A. E., Bakarr, M., Bicksler, A. J., Galt, R., Garibaldi, L. A., Gemmill-Herren, B., Grass, I., Isaac, M. E., John, I., Jones, S. K., Kennedy, C. M., ... Kremen, C. (2023). Against the odds: Pathways to agricultural diversification. *One Earth*, 6, 479–491.
- Borden, K. A., Anglaaere, L. C. N., Owusu, S., Martin, A. R., Buchanan, S. W., Addo-Danso, S. D., & Isaac, M. E. (2020). Soil texture moderates root functional traits in agroforestry systems across a climatic gradient. *Agriculture, Ecosystems & Environment*, 295, 106915. <https://doi.org/10.1016/j.agee.2020.106915>
- Borden, K. A., Thomas, S. C., & Isaac, M. E. (2020). Variation in fine root traits reveals nutrient-specific acquisition strategies in agroforestry systems. *Plant and Soil*, 453(1–2), 139–151. <https://doi.org/10.1007/s11104-019-04003-2>
- Buchanan, S., Isaac, M. E., Van den Meersche, K., & Martin, A. R. (2019). Functional traits of coffee den along a shade and fertility gradient in coffee agroforestry systems. *Agroforestry Systems*, 93(4), 1261–1273. <https://doi.org/10.1007/s10457-018-0239-1>
- Cardinael, R., Chevallier, T., Cambou, A., Béal, C., Barthès, B. G., Dupraz, C., Durand, C., Kouakoua, E., & Chenu, C. (2017). Increased soil organic carbon stocks under agroforestry: A survey of six different sites in France. *Agriculture, Ecosystems & Environment*, 236, 243–255. <https://doi.org/10.1016/j.agee.2016.12.011>
- Cardinael, R., Hoeffner, K., Chenu, C., Chevallier, T., Béal, C., Dewisme, A., & Cluzeau, D. (2019). Spatial variation of earthworm communities and soil organic carbon in temperate agroforestry. *Biology and Fertility of Soils*, 55(2), 171–183. <https://doi.org/10.1007/s00374-018-1332-3>
- Carminati, A., & Javaux, M. (2020). Soil rather than xylem vulnerability controls stomatal response to drought. *Trends in Plant Science*, 25(9), 868–880. <https://doi.org/10.1016/j.tplants.2020.04.003>
- Cerdan, C. R., Rebolledo, M. C., Soto, G., Rapidel, B., & Sinclair, F. L. (2012). Local knowledge of impacts of tree cover on ecosystem services in smallholder coffee production systems. *Agricultural Systems*, 110, 119–130. <https://doi.org/10.1016/j.agee.2012.03.014>
- Charbonnier, F., Le Maire, G., Dreyer, E., Casanoves, F., Christina, M., Dauzat, J., Eitel, J. U. H., Vaast, P., Vierling, L. A., & Roupard, O. (2013). Competition for light in heterogeneous canopies: Application of MAESTRA to a coffee (*Coffea arabica* L.) agroforestry system. *Agriculture and Forest Meteorology*, 181, 152–169.

- Charbonnier, F., Rounsard, O., le Maire, G., Guillemot, J., Casanoves, F., Lacoite, A., Vaast, P., Allinne, C., Audebert, L., Cambou, A., Clément-Vidal, A., Defrenet, E., Duursma, R. A., Jarri, L., Jourdan, C., Khac, E., Leandro, P., Medlyn, B. E., Saint-André, L., ... Dreyer, E. (2017). Increased light-use efficiency sustains net primary productivity of shaded coffee plants in agroforestry system. *Plant, Cell & Environment*, 40(8), 1592–1608. <https://doi.org/10.1111/pce.12964>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chaves, A. R. M., Ten-Caten, A., Pinheiro, H. A., Ribeiro, A., & DaMatta, F. (2008). Seasonal changes in photoprotective mechanisms of leaves from shaded and unshaded field-grown coffee (*Coffea arabica* L.) trees. *Trees*, 22, 351–361. <https://doi.org/10.1007/s00468-007-0190-7>
- Chiam, Z., Song, X. P., Lai, H. R., & Tan, H. T. W. (2019). Particulate matter mitigation via plants: Understanding complex relationships with leaf traits. *Science of the Total Environment*, 688, 398–408. <https://doi.org/10.1016/j.scitotenv.2019.06.263>
- Cleugh, H. A. (1998). Effects of windbreaks on airflow, microclimates and crop yields. *Agroforestry Systems*, 41, 55–84. <https://doi.org/10.1023/A:1006019805109>
- Corada, K., Woodward, H., Alaraj, H., Collins, C. M., & de Nazelle, A. (2021). A systematic review of the leaf traits considered to contribute to removal of airborne particulate matter pollution in urban areas. *Environmental Pollution*, 269, 116104. <https://doi.org/10.1016/j.envpol.2020.116104>
- Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79(1), 109–126. <https://doi.org/10.1890/07-1134.1>
- Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Queded, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., Van Bodegom, P., Brovkin, V., Chatain, A., ... Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11(10), 1065–1071. <https://doi.org/10.1111/j.1461-0248.2008.01219.x>
- Correa, D. F., Stevenson, P. R., Umaña, M. N., Coelho, L. D. S., Lima Filho, D. D. A., Salomão, R. P., do Amaral, I. L., et al. (2023). Geographic patterns of tree dispersal modes in Amazonia and their ecological correlates. *Global Ecology and Biogeography*, 32, 49–69. <https://doi.org/10.1111/geb.13596>
- da Silva Neto, F. J., Morinigo, K. P. G., de França Guimarães, N., de Souza Gallo, A., de Souza, M. D. B., Stolf, R., & Anastácia, F. (2018). Shade trees spatial distribution and its effect on grains and beverage quality of shaded coffee trees. *Journal of Food Quality*, 2018, 1–8. <https://doi.org/10.1155/2018/7909467>
- Daghela Bisseleua, H. B., Fotio, D., Yede, Missoup, A. D., & Vidal, S. (2013). Shade tree diversity, cocoa pest damage, yield compensating inputs and farmers net returns in West Africa. *PLoS One*, 8(3), e56115. <https://doi.org/10.1371/journal.pone.0056115>
- DaMatta, F. (2004). Ecophysiological constraints on the production of shaded and unshaded coffee: A review. *Field Crops Research*, 86, 99–114.
- Djuideu, C. T. L., Bisseleua, H. D. B., Kekeunou, S., & Ambele, F. C. (2021). Rehabilitation practices in cocoa agroforestry systems mitigate outbreaks of termites and support cocoa tree development and yield. *Agriculture, Ecosystems & Environment*, 311, 107324. <https://doi.org/10.1016/j.agee.2021.107324>
- Dollinger, J., & Jose, S. (2018). Agroforestry for soil health. *Agroforestry Systems*, 92(2), 213–219. <https://doi.org/10.1007/s10457-018-0223-9>
- Dzierżanowski, K., Popek, R., Gawrońska, H., Sæbø, A., & Gawroński, S. W. (2011). Deposition of particulate matter of different size fractions on leaf surfaces and in waxes of urban forest species. *International Journal of Phytoremediation*, 13(10), 1037–1046. <https://doi.org/10.1080/15226514.2011.552929>
- Esquivel, M. J., Vilchez-Mendoza, S., Harvey, C. A., Ospina, M. A., Somarriba, E., Deheuvels, O., de Melo Virginio Filho, E., Hagggar, J., Detlefsen, G., Cerdan, C., Casanoves, F., & Ordoñez, J. C. (2023). Patterns of shade plant diversity in four agroforestry systems across Central America: A meta-analysis. *Scientific Reports*, 13, 8538. <https://doi.org/10.1038/s41598-023-35578-7>
- Estrada-Carmona, N., Martínez-Salinas, A., Declerck, F., Vilchez-Mendoza, S., & Garbach, K. (2019). Managing the farmscape for connectivity increases conservation value for tropical bird species with different forest-dependencies. *Journal of Environmental Management*, 250, 109504. <https://doi.org/10.1016/j.jenvman.2019.109504>
- Falster, D. S., & Westoby, M. (2005). Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. *Oikos*, 111, 57–66. <https://doi.org/10.1111/j.0030-1299.2005.13383.x>
- Fang, H., Baret, F., Plummer, S., & Strub, G. S. (2019). An overview of global leaf area index (LAI): Methods, products, validation, and applications. *Reviews of Geophysics*, 57, 739–799. doi:10.1029/2018rg000608
- Finney, D., & Kaye, J. (2016). Functional diversity in cover crop polycultures increases multifunctionality of an agricultural system. *Journal of Applied Ecology*, 54, 509–517. <https://doi.org/10.1111/1365-2664.12765>
- Funk, J. L., Larson, J. E., Ames, G. B., Butterfield, B. J., Cavender-Bares, J., Finn, J., Laughlin, D. C., Sutton-Grier, A. E., Williams, L., & Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, 92(2), 1156–1173. <https://doi.org/10.1111/brv.12275>
- Gagliardi, S., Avelino, J., Beilhe, L. B., & Isaac, M. E. (2020). Contribution of shade trees to wind dynamics and pathogen dispersal on the edge of coffee agroforestry systems: A functional traits approach. *Crop Protection*, 130, 105071. <https://doi.org/10.1016/j.cropro.2019.105071>
- Gagliardi, S., Avelino, J., de Melo Virginio Filho, E., & Isaac, M. E. (2021). Shade tree traits and microclimate modifications: Implications for pathogen management in biodiverse coffee agroforests. *Biotropica*, 53(5), 1356–1367. <https://doi.org/10.1111/btp.12984>
- Gagliardi, S., Avelino, J., Martin, A. R., Cadotte, M., de Melo Virginio Filho, E., & Isaac, M. E. (2023). Leaf functional traits and pathogens: Linking coffee leaf rust with intraspecific trait variation in diversified agroecosystems. *PLoS One*, 18(4), e0284203. <https://doi.org/10.1371/journal.pone.0284203>
- Gagliardi, S., Martin, A. R., de Melo Virginio Filho, E., Rapidel, B., & Isaac, M. E. (2015). Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes. *Agriculture, Ecosystems & Environment*, 200, 151–160. <https://doi.org/10.1016/j.agee.2014.11.014>
- Garnier, E., Cortez, J., Billes, B., Navas, M. L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J. P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85(9), 2630–2637. <https://doi.org/10.1890/03-0799>
- Geißler, C., Nadrowski, K., Kühn, P., Baruffol, M., Bruelheide, H., Schmid, B., & Scholten, T. (2013). Kinetic energy of throughfall in subtropical forests of SE China—Effects of tree canopy structure, functional traits, and biodiversity. *PLoS One*, 8(2), e49618. <https://doi.org/10.1371/journal.pone.0049618>
- Getachew, M., Verheyen, K., Tolassa, K., Tack, A. J. M., Hylander, K., Ayalew, B., Boeckx, P., Landuyt, D., & De Frenne, P. (2023). Effects of shade tree species on soil biogeochemistry and

- coffee bean quality in plantation coffee. *Agriculture, Ecosystems & Environment*, 347, 108354. <https://doi.org/10.1016/j.agee.2023.108354>
- Gómez, J. A., Giráldez, J. V., & Fereres, E. (2001). Rainfall interception by olive trees in relation to leaf area. *Agricultural Water Management*, 49(1), 65–76. [https://doi.org/10.1016/S0378-3774\(00\)00116-5](https://doi.org/10.1016/S0378-3774(00)00116-5)
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *The Journal of Ecology*, 86(6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, B., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. *Nature Ecology & Evolution*, 1(5), 0132. <https://doi.org/10.1038/s41559-017-0132>
- Guillot, E., Bertrand, I., Rumpel, C., Gomez, C., Arnal, D., Abadie, J., & Hinsinger, P. (2021). Spatial heterogeneity of soil quality within a Mediterranean alley cropping agroforestry system: Comparison with a monocropping system. *European Journal of Soil Biology*, 105, 103330. <https://doi.org/10.1016/j.ejsobi.2021.103330>
- Häger, A., & Avalos, G. (2017). Do functional diversity and trait dominance determine carbon storage in an altered tropical landscape? *Oecologia*, 184(2), 569–581. <https://doi.org/10.1007/s00442-017-3880-x>
- Haggar, J., Aguirrez, M., Bolaños, M., Merlo, M., Moraga, P., Munguia, R., Ponce, A., Romero, S., Soto, G., Staver, C., & de Melo Virginio Filho, E. (2011). Coffee agroecosystem performance under full sun, shade, conventional and organic management regimes in Central America. *Agroforestry Systems*, 82, 285–301. <https://doi.org/10.1007/s10457-011-9392-5>
- Harvey, C. A., Komar, O., Chazdon, R., Ferguson, B. G., Finegan, B., Griffith, D. M., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Van Breugel, M., & Wishnie, M. (2008). Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. *Conservation Biology*, 22(1), 8–15.
- Isaac, M. E., & Borden, K. A. (2019). Nutrient acquisition strategies in agroforestry systems. *Plant and Soil*, 444, 1–19. <https://doi.org/10.1007/s11104-019-04232-5>
- Isaac, M. E., Cerda, R., Rapidel, B., Martin, A. R., Dickinson, A. K., & Sibelet, N. (2018). Farmer perception and utilization of leaf functional traits in agroecosystems. *Journal of Applied Ecology*, 55, 69–80. <https://doi.org/10.1111/1365-2664.13027>
- Isaac, M. E., Nyantakyi-Frimpong, H., Matous, P., Dawoe, E., & Anglaaere, L. (2021). Farmer networks and agrobiodiversity interventions: the unintended outcomes of intended change. *Ecology and Society*, 26(4). <https://doi.org/10.5751/ES-12734-260412>
- Isaac, M. E., Timmer, V. R., & Quashie-Sam, S. J. (2007). Shade tree effects in an 8-year-old cocoa agroforestry system: Biomass and nutrient diagnosis of *Theobroma cacao* by vector analysis. *Nutrient Cycling in Agroecosystems*, 78(2), 155–165. <https://doi.org/10.1007/s10705-006-9081-3>
- Jaramillo-Botero, C., Santos, R., Prieto, M., Cecon, P., & Fardin, M. (2010). Production and vegetative growth of coffee trees under fertilization and shade levels. *Scientia Agricola*, 67, 639–645. <https://doi.org/10.1590/S0103-90162010000600004>
- Jin, E. J., Yoon, J. H., Bae, E. J., Jeong, B. R., Yong, S. H., & Choi, M. S. (2021). Particulate matter removal ability of ten evergreen trees planted in Korea Urban Greening. *Forests*, 12(4), 438. <https://doi.org/10.3390/f12040438>
- Jose, S. (2009). Agroforestry for ecosystem services and environmental benefits: An overview. *Agroforestry Systems*, 76, 1–10. <https://doi.org/10.1007/s10457-009-9229-7>
- Kattge, J., Bönsch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Banerjee, A., Boonman, C. C. F., Feng, Y., Muller, S., Ozinga, W. A., Robroek, B. J. M., Zhao, Y., Zotz, G., & Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. <https://doi.org/10.1111/gcb.14904>
- Kim, D.-G., & Isaac, M. E. (2022). Nitrogen dynamics in agroforestry systems: A review with data synthesis. *Agronomy for Sustainable Development*, 42, 1–18.
- Koko, L. K., Snoeck, D., Lekadou, T. T., & Assiri, A. A. (2013). Cacao-fruit tree intercropping effects on cocoa yield, plant vigour and light interception in Côte d'Ivoire. *Agroforestry Systems*, 87, 1043–1052.
- Kraft, N. J. B., & Ackerly, D. D. (2014). Assembly of Plant Communities. In R. K. Monson (Ed.), *Ecology and the Environment* (pp. 67–88). Springer.
- Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322(5901), 580–582. <https://doi.org/10.1126/science.1160662>
- Lal, R. (2004). Soil carbon sequestration impacts on global climate change and food security. *Science*, 304(5677), 1623–1627. <https://doi.org/10.1126/science.1097396>
- Lavoral, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 15, 545–556.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrrough, J., Berman, S., Quétiér, F., Thébault, A., & Bonis, A. (2008). Assessing functional diversity in the field—Methodology matters! *Functional Ecology*, 22, 134–147.
- Lin, B. B. (2007). Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. *Agricultural and Forest Meteorology*, 144(1–2), 85–94. <https://doi.org/10.1016/j.agrformet.2006.12.009>
- Liu, J., Liu, W., & Zhu, K. (2018). Throughfall kinetic energy and its spatial characteristics under rubber-based agroforestry systems. *Catena*, 161, 113–121. <https://doi.org/10.1016/j.catena.2017.10.014>
- Lohbeck, M., Poorter, L., Paz, H., Pla, L., van Breugel, M., Martínez-Ramos, M., & Bongers, F. (2012). Functional diversity changes during tropical forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*, 14, 89–96. <https://doi.org/10.1016/j.ppees.2011.10.002>
- López-Bravo, D. F., de Melo Virginio Filho, E., & Avelino, J. (2012). Shade is conducive to coffee rust as compared to full sun exposure under standardized fruit load conditions. *Crop Protection*, 38, 21–29. <https://doi.org/10.1016/j.cropro.2012.03.011>
- Loranger, J., Meyer, S. T., Shipley, B., Kattge, J., Loranger, H., Roscher, C., & Weisser, W. W. (2012). Predicting invertebrate herbivory from plant traits: Evidence from 51 grassland species in experimental monocultures. *Ecology*, 93(12), 2674–2682. <https://doi.org/10.1890/12-0328.1>
- Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü., Ordóñez, A., Reich, P. B., & Santiago, L. S. (2015). Global effects of soil and climate on leaf photosynthetic traits and rates. *Global Ecology and Biogeography*, 24(6), 706–717. <https://doi.org/10.1111/geb.12296>
- Malézieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., Tourdonnet, S., & Valantin-Morison, M. (2009). Mixing plant species in cropping systems: Concepts, tools and models: A review. *Agronomy for Sustainable Development*, 29, 43–62.
- Martin, A. R., & Isaac, M. E. (2015). Plant functional traits in agroecosystems: A blueprint for research. *Journal of Applied Ecology*, 52(6), 1425–1435. <https://doi.org/10.1111/1365-2664.12526>
- Martin, A. R., & Isaac, M. E. (2021). The leaf economics spectrum's morning coffee: Plant size-dependent changes in leaf traits and reproductive onset in a perennial tree crop. *Annals of Botany*, 127(4), 483–493.
- Martin, A. R., Rapidel, B., Rouspard, O., den Meersche, K. V., de Melo Virginio Filho, E., Barrios, M., & Isaac, M. E. (2017). Intraspecific trait variation across multiple scales: The leaf economics spectrum

- in coffee. *Functional Ecology*, 31(3), 604–612. <https://doi.org/10.1111/1365-2435.12790>
- Mason, N. W. H., Mouillot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111(1), 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Méndez, V. E., Shapiro, E. N., & Gilbert, G. S. (2009). Cooperative management and its effects on shade tree diversity, soil properties and ecosystem services of coffee plantations in western El Salvador. *Agroforestry Systems*, 76(1), 111–126. <https://doi.org/10.1007/s10457-009-9220-3>
- Merle, I., Villarreyna-Acuña, R., Ribeyre, F., Rouspard, O., Cilas, C., & Avelino, J. (2022). Microclimate estimation under different coffee-based agroforestry systems using full-sun weather data and shade tree characteristics. *European Journal of Agronomy*, 132(August 2020), 126396. <https://doi.org/10.1016/j.eja.2021.126396>
- Meylan, L., Gary, C., Allinne, C., Ortiz, J., Jackson, L., & Rapidel, B. (2017). Evaluating the effect of shade trees on provision of ecosystem services in intensively managed coffee plantations. *Agriculture Ecosystems and Environment*, 245, 32–42.
- Miyaji, K.-I., da Silva, W. S., & de Alvim, P. T. (1997). Productivity of leaves of a tropical tree, *Theobroma cacao*, grown under shading, in relation to leaf age and light conditions within the canopy. *The New Phytologist*, 137(3), 463–472. <https://doi.org/10.1046/j.1469-8137.1997.00841.x>
- Moço, M. K. S., Gama-Rodrigues, E. F., Gama-Rodrigues, A. C., Machado, R. C. R., & Baligar, V. C. (2010). Relationships between invertebrate communities, litter quality and soil attributes under different cacao agroforestry systems in the south of Bahia, Brazil. *Applied Soil Ecology*, 46(3), 347–354. <https://doi.org/10.1016/j.apsoil.2010.10.006>
- Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T., & Westoby, M. (2007). Global patterns in seed size. *Global Ecology and Biogeography*, 16(1), 109–116. <https://doi.org/10.1111/j.1466-8238.2006.00259.x>
- Moles, A. T., & Leishman, M. R. (2008). The seedling as part of a plant's life history strategy. In M. A. Leck, R. L. Simpson, & V. T. Parker (Eds.), *Seedling ecology and evolution* (pp. 217–238). Cambridge University Press.
- Muchane, M. N., Sileshi, G. W., Gripenberg, S., Jonsson, M., Pumarino, L., & Barrios, E. (2020). Agroforestry boosts soil-mediated ecosystem services in the humid and sub-humid tropics: A meta-analysis. *Agriculture, Ecosystems and Environment*, 295, 106899. <https://doi.org/10.1016/j.agee.2020.106899>
- Muleta, D., Assefa, F., Nemomissa, S., & Granhall, U. (2007). Composition of coffee shade tree species and density of indigenous arbuscular mycorrhizal fungi (AMF) spores in Bonga natural coffee forest, southwestern Ethiopia. *Forest Ecology and Management*, 241(1), 145–154. <https://doi.org/10.1016/j.foreco.2007.01.021>
- Nanko, K., Hotta, N., & Suzuki, M. (2006). Evaluating the influence of canopy species and meteorological factors on throughfall drop size distribution. *Journal of Hydrology*, 329(3–4), 422–431. <https://doi.org/10.1016/j.jhydrol.2006.02.036>
- Niether, W., Armengot, L., Andres, C., Schneider, M., & Gerold, G. (2018). Shade trees and tree pruning alter throughfall and microclimate in cocoa (*Theobroma cacao* L.) production systems. *Annals of Forest Science*, 75, 1–16.
- Niether, W., Jacobi, J., Blaser, W. J., Andres, C., & Armengot, L. (2020). Cocoa agroforestry systems versus monocultures: A multi-dimensional meta-analysis. *Environmental Research Letters*, 15, 104085.
- Nimmo, V., Violle, C., Entz, M., Rolhauser, A., & Isaac, M. E. (2023). Changes in crop trait plasticity with domestication history: Management practices matter. *Ecology and Evolution*, 11, e10690. <https://doi.org/10.1002/ece3.10690>
- Ordóñez, J. C., Luedeling, E., Kindt, R., Tata, H. L., Harja, D., Jamnadass, R., & van Noordwijk, M. (2014). Constraints and opportunities for tree diversity management along the forest transition curve to achieve multifunctional agriculture. *Current Opinion in Environmental Sustainability*, 6, 54–60.
- Ordoñez, J. C., Van Bodegom, P. M., Witte, J. P. M., Wright, I. J., Reich, P. B., & Aerts, R. (2009). A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, 18(2), 137–149. <https://doi.org/10.1111/j.1466-8238.2008.00441.x>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., De Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167–234. <https://doi.org/10.1071/BT12225>
- Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, 9(6), 741–758. <https://doi.org/10.1111/j.1461-0248.2006.00924.x>
- Piato, K., Lefort, F., Subía, C., Caicedo, C., Calderón, D., Pico, J., & Norgrove, L. (2020). Effects of shade trees on robusta coffee growth, yield and quality: A meta-analysis. *Agronomy for Sustainable Development*, 40, 38. <https://doi.org/10.1007/s13593-020-00642-3>
- Rahn, E., Vaast, P., Läderach, P., Van Asten, P., Jassogne, L., & Ghazoul, J. (2018). Exploring adaptation strategies of coffee production to climate change using a process-based model. *Ecological Modelling*, 371, 76–89.
- Ramírez-Argueta, O., Orozco-Aguilar, L., Dubón, A. D., Díaz, F. J., Sánchez, J., & Casanoves, F. (2022). Timber growth, cacao yields, and financial revenues in a long-term experiment of cacao agroforestry systems in northern Honduras. *Frontiers in Sustainable Food Systems*, 6, 941743. <https://doi.org/10.3389/fsufs.2022.941743>
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, 94(25), 13730–13734. <https://doi.org/10.1073/pnas.94.25.13730>
- Rigal, C., Wagner, S., Nguyen, M. P., Jassogne, L., & Vaast, P. (2022). ShadeTreeAdvice methodology: Guiding tree-species selection using local knowledge. *People and Nature*, 4, 1233–1248. <https://doi.org/10.1002/pan3.10374>
- Rodríguez-López, N. F., Martins, S. C., Cavatte, P. C., Silva, P. E., Morais, L. E., Pereira, L. F., Reis, J. V., Ávila, R. T., Godoy, A. G., Lavinski, A. O., & DaMatta, F. M. (2014). Morphological and physiological acclimations of coffee seedlings to growth over a range of fixed or changing light supplies. *Environmental and Experimental Botany*, 102, 1–10.
- Rolhauser, A., Windfeld, E., Hanson, S., Wittman, H., Thoreau, C., Lyon, A., & Isaac, M. E. (2022). A trait-environment relationship approach to participatory plant breeding for organic agriculture. *New Phytologist*, 235, 1018–1031.
- Romero-Alvarado, Y., Soto-Pinto, L., García-Barríos, L., & Barrera-Gaytán, J. F. (2002). Coffee yields and soil nutrients under the shades of Inga sp. vs. multiple species in Chiapas, Mexico. *Agroforestry Systems*, 54, 215–224. <https://doi.org/10.1023/A:1016013730154>

- Rousseau, G. X., Deheuvels, O., Celentano, D., Arias, I. R., Hernández-García, L. M., & Somarriba, E. (2021). Shade tree identity rather than diversity influences soil macrofauna in cacao-based agroforestry systems. *Pedobiologia*, 89, 150770. <https://doi.org/10.1016/j.pedobi.2021.150770>
- Sauvadet, M., Asare, R., & Isaac, M. E. (2020). Evolutionary distance explains shade tree selection in agroforestry systems. *Agriculture, Ecosystems and Environment*, 304, 107125.
- Sauvadet, M., den Meersche, K. V., Allinne, C., Gay, F., de Melo Virgínio Filho, E., Chauvat, M., Becquer, T., Tixier, P., & Harmand, J.-M. (2019). Shade trees have higher impact on soil nutrient availability and food web in organic than conventional coffee agroforestry. *Science of the Total Environment*, 649, 1065–1074. <https://doi.org/10.1016/j.scitotenv.2018.08.291>
- Sauvadet, M., Dickinson, A. K., Somarriba, E., Phillips-Mora, W., Cerda, R. H., Martin, A. R., & Isaac, M. E. (2021). Genotype-environment interactions shape leaf functional traits of cacao in agroforests. *Agronomy for Sustainable Development*, 41, 1–12. <https://doi.org/10.1007/s13593-021-00690-03>
- Sauvadet, M., Saj, S., Freschet, G. T., Essobo, J.-D., Enock, S., Becquer, T., Tixier, P., & Harmand, J.-M. (2020). Cocoa agroforest multifunctionality and soil fertility explained by shade tree litter traits. *Journal of Applied Ecology*, 57(3), 476–487. <https://doi.org/10.1111/1365-2664.13560>
- Sewnet, T. C., & Tuju, F. A. (2013). Arbuscular mycorrhizal fungi associated with shade trees and *Coffea arabica* L. in a coffee-based agroforestry system in Bonga, Southwestern Ethiopia. *Afrika Focus*, 26(2), 111–131. <https://doi.org/10.1163/2031356X-02602007>
- Shiple, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, 180(4), 923–931. <https://doi.org/10.1007/s00442-016-3549-x>
- Shiple, B., Vile, D., Garnier, E., Wright, I. J., & Poorter, H. (2005). Functional linkages between leaf traits and net photosynthetic rate: Reconciling empirical and mechanistic models. *Functional Ecology*, 19, 602–615.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W., Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., Dantas, V. d. L., de Bello, F., Duarte, L. D. S., Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., ... Chase, J. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406–1419. <https://doi.org/10.1111/ele.12508>
- Siles, P., Vaast, P., Dreyer, E., & Harmand, J. M. (2010). Rainfall partitioning into throughfall, stemflow and interception loss in a coffee (*Coffea arabica* L.) monoculture compared to an agroforestry system with *Inga densiflora*. *Journal of Hydrology*, 395(1–2), 39–48. <https://doi.org/10.1016/j.jhydrol.2010.10.005>
- Somarriba, E., Beer, J., Orihuela, J. A., Andrade, H., Cerda, R., DeClerck, F., Detlefsen, G., Escalante, M., Giraldo, L. A., Ibrahim, M., Krishnamurthy, L., Mena, V. E., Mora-Delgado, J., Orozco, L., Scheelje, M., & Campos, J. J. (2012). Mainstreaming agroforestry in Latin America. In P. K. R. Nair & D. P. Garrity (Eds.), *Agroforestry: The way forward. Advances in agroforestry* 9 (pp. 429–453). Springer.
- Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., Van Der Heijden, M. G., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, 6(45), eaba1715.
- Tezara, W., Pereyra, G., Ávila-Lovera, E., & Herrera, A. (2020). Variability in physiological responses of Venezuelan cacao to drought. *Experimental Agriculture*, 56(3), 407–421. <https://doi.org/10.1017/S0014479720000058>
- Tscharntke, T., Clough, Y., Bhagwat, S. A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., & Wanger, T. C. (2011). Multifunctional shade-tree management in tropical agroforestry landscapes—A review. *Journal of Applied Ecology*, 48(3), 619–629. <https://doi.org/10.1111/j.1365-2664.2010.01939.x>
- Vaast, P., Harmand, J. M., Rapidel, B., Jagoret, P., & Deheuvels, O. (2016). Coffee and cocoa production in agroforestry—A climate-smart agriculture model. In (E. Torquebiau (Ed.), D. Manley (Trad.), & P. Cowan (Trad.)) In *Climate change and agriculture worldwide* (pp. 209–224). Springer.
- Vaast, P., Kanten, R., Siles, P., & Angrand, J. (2008). Biophysical interactions between timber trees and Arabica coffee in suboptimal conditions of Central America. In S. Jose & A. M. Gordon (Eds.), *Toward agroforestry design: An ecological approach* (4th ed., pp. 133–146). Springer. [https://doi.org/10.1007/978-1-4020-6572-9\\_9](https://doi.org/10.1007/978-1-4020-6572-9_9)
- van Oijen, M., Dauzat, J., Harmand, J.-M., Lawson, G., & Vaast, P. (2010). Coffee agroforestry systems in Central America: I. A review of quantitative information on physiological and ecological processes. *Agroforestry Systems*, 80(3), 341–359. <https://doi.org/10.1007/s10457-010-9294-y>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>
- Vogel, S. (1989). Drag and reconfiguration of broad leaves in high winds. *Journal of Experimental Botany*, 40(8), 941–948. <https://doi.org/10.1093/jxb/40.8.941>
- Wallwork, A., Banin, L. F., Dent, D. H., Skiba, U., & Sayer, E. (2022). Soil carbon storage is related to tree functional composition in naturally regenerating tropical forests. *Functional Ecology*, 36(12), 3175–3187. <https://doi.org/10.1111/1365-2435.14221>
- Wartenberg, A. C., Blaser, W. J., Roshetko, J. M., Van Noordwijk, M., & Six, J. (2020). Soil fertility and Theobroma cacao growth and productivity under commonly intercropped shade-tree species in Sulawesi, Indonesia. *Plant and Soil*, 453(1–2), 87–104. <https://doi.org/10.1007/s11104-018-03921-x>
- Weedon, J. T., Cornwell, W. K., Cornelissen, J. H. C., Zanne, A. E., Wirth, C., & Coomes, D. A. (2009). Global meta-analysis of wood decomposition rates: A role for trait variation among tree species? *Ecology Letters*, 12(1), 45–56. <https://doi.org/10.1111/j.1461-0248.2008.01259.x>
- Westerband, A. C., Funk, J. L., & Barton, K. E. (2021). Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. *Annals of Botany*, 127(4), 397–410. <https://doi.org/10.1093/aob/mcab011>
- Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33(1), 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*, 21(5), 261–268. <https://doi.org/10.1016/j.tree.2006.02.004>
- Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I., & Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by climate. *Global Ecology and Biogeography*, 14(5), 411–421. <https://doi.org/10.1111/j.1466-822x.2005.00172.x>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gullas, J., Hikosaka, K.,

- Lamont, B. B., Lee, T., Lusk, C., Midgley, J. J., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. doi:[10.1038/nature02403](https://doi.org/10.1038/nature02403)
- Zhang, W., Liu, W., Li, W., Zhu, X., Chen, C., Zeng, H., Jiang, X., Singh, A. K., & Yang, B. (2021). Characteristics of throughfall kinetic energy under the banana (*Musa nana* Lour.) canopy: The role of leaf shapes. *Catena*, 197, 104985. <https://doi.org/10.1016/j.catena.2020.104985>

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## SUPPORTING INFORMATION

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

**Supporting Information S1.** Supporting information.