



Short communication

## Evolutionary distance explains shade tree selection in agroforestry systems

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## ABSTRACT

Enhancing agrobiodiversity offers a suite of functions key to the sustainability of low input agroecosystems. The pairing of shade trees in pan-tropical tree-crop systems represents one of the most common and widespread applications of agroecosystem diversification, yet given the vastly heterogeneous conditions in which shade tree selection is made, generalizable advances in the identification of suitably paired tree-crop and shade tree is essential for performance and adoption. Here, we determine the phylogenetic distance between 78 reported shade tree genera and the dominant tree-crop, *Theobroma cacao* L (cocoa), across four countries in sub-Saharan Africa. We hypothesize that shade trees classified as desirable will be phylogenetically distant from *T. cacao*, based on the well-established theory that disparate evolutionary histories confer niche differentiation. Our analyses confirm that shade tree taxa categorized as desirable by farmers and institutions present higher phylogenetic distance with *T. cacao* than shade trees taxa categorized as undesirable. These results demonstrate that shade tree evolutionary distance to the target crop could be a useful tool to predict a taxon's *a priori* suitability in cocoa agroforests, as well as the ability of phylogenetic analyses in prescribing appropriate shade trees in other current and future agroforestry systems.

## 1. Introduction

Research focusing on biologically complex systems strongly suggests that greater diversity in agroecosystems leads to higher ecosystem functioning, such as productivity and efficient nutrient cycling (Kremen and Miles, 2012; Martin and Isaac, 2015). The pairing of tree-crops with shade trees is one of the most common and widespread applications of diversification in agroecosystems. For instance, cocoa (*Theobroma cacao*) agroforestry systems comprise 31% of the 10 mil ha of land under cocoa cultivation globally (Somarrriba and López Sampson, 2018). Mounting evidence supports a suite of ecosystem functions and services derived from these pairings, including yield stability, climate regulation, disease mitigation, localized soil fertility, and the production of food (Vaast et al., 2016; Andres et al., 2018; Somarrriba and López Sampson, 2018; Borden et al., 2020). Major advances have been made in diagnosing and prescribing the 'right' shade tree for these systems based on: i) shade tree phenology and canopy exposure (Asare and Anders, 2016), ii) the climatic envelope (Abdulai et al., 2018), and iii) soil health (Isaac and Borden, 2019). Notably, while these filters are often the basis of scientific enquiry, they also underpin locally developed, and highly

nuanced, knowledge of shade tree desirability (Isaac et al., 2009; Niether et al., 2019).

Given the vastly heterogeneous conditions in which shade tree selection is made, and the inconsistent, and sometimes conflicting, evidence on the benefits of cocoa agroforestry (Ruf, 2011; Blaser et al., 2017), advances in the identification of suitably paired tree-crop and shade tree are required. Essential to this successful selection of species combinations in diversified agroecosystems is the ecological fit between species. Community ecologists have tackled this issue with a suite of theory-based measures that underpin the role of species differences in their ability to confer complementarity or facilitation. These ecological similarities or differences can be described by taxonomy (Hooper et al., 2005), functional diversity (Martin and Isaac, 2015), and phylogenetic diversity (Srivastava et al., 2012). In particular, phylogenetic diversity (the evolutionary history between species) has been shown to explain a suite of ecosystem functions, to a greater extent than species richness alone (Cadotte et al., 2012). In essence, the greater the evolutionary distance between species, the higher the likelihood of niche differentiation. While such measures have been applied extensively to natural communities (Flynn et al., 2011), and more recently to diversification of crop

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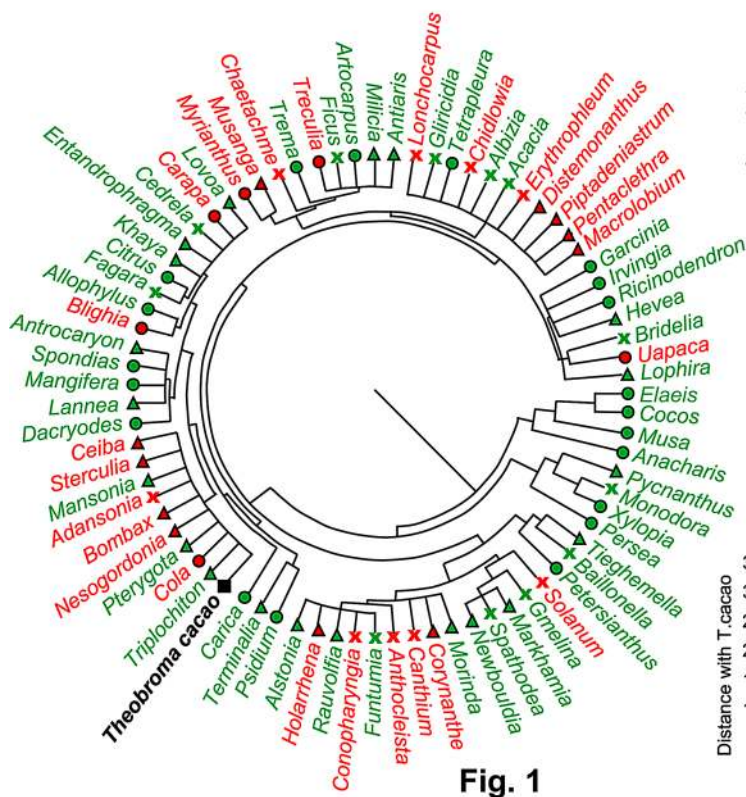
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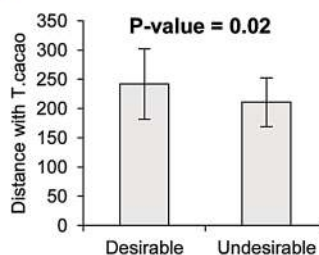
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**Fig. 1**

**Fig. 1.** Phylogenetic tree of shade tree genera in *Theobroma cacao* (cocoa) agroforestry systems in four countries of sub-Saharan Africa. Shade tree genera classified as desirable are in green, and shade tree genera classified as undesirable are in red. Tip edge shape indicates the dominant shade tree use (circle = food crops; triangle = timber; cross = other). The mean (+/- SD) shade tree genera dissimilarity with *T. cacao* between desirability status is presented in the bar graph. Total number of shade tree genera and Faith's index are also provided.



rotations (Ingerslew and Kaplan, 2018; Kaplan et al., 2020), evolutionary based measurements have seldom been used to elucidate optimal shade tree selection and functioning in diversified agroforestry systems.

Here, we provide a novel analysis by pairing the perception, experience and inventory of shade tree preference with shade tree evolutionary history within agroforestry systems. We determine the phylogenetic distance between 78 reported shade tree genera and the dominant tree-crop, *Theobroma cacao*, across four countries in sub-Saharan Africa. We hypothesize that phylogenetic distance between *T. cacao* and shade trees classified as 'desirable' (by farmers and institutions) will be greater than the distance between *T. cacao* and 'undesirable' shade trees. This hypothesis is based on the well-established theory that disparate evolutionary histories confer niche differentiation. Our findings point to the significant ability of phylogenetic analyses in prescribing appropriate shade trees in current and future agroforestry systems.

**2. Material and Methods**

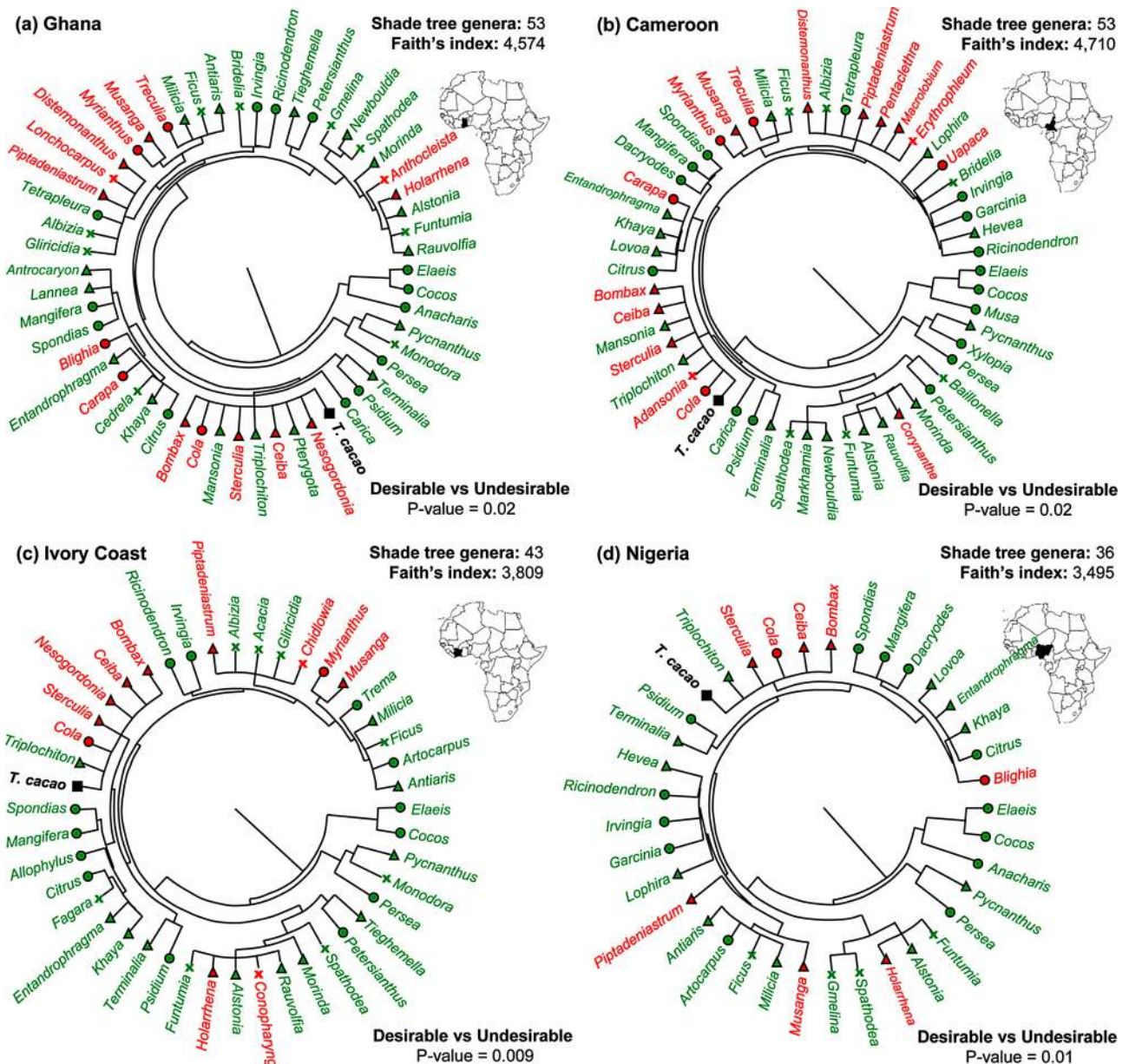
We consolidated shade tree taxa in sub-Saharan African cocoa farms from four countries: Ghana, Cameroon, Ivory Coast and Nigeria. To achieve this, we populated a species list from two sources: shade tree recommendations from official institutes [e.g. CRIG (Cocoa Research Institute of Ghana) or CCC (Le Conseil du Café-Cacao)], and a systematic review of scholarly literature on shade tree species in cocoa agroforests. References based solely on shade tree frequency in farms were discarded; frequency can obfuscate preference as presence may simply be due to difficult removal during field establishment (Herzog, 1994). The data were then aggregated at the genus level to i) account for several references assessing shade tree desirability at this taxonomic level (UTZ, 2017), and ii) limit the imbalance caused by an over-representation of some genera (for instance, 14 species from the *Cola* genus were described). We restricted our list to taxa paired with recommendations

on their benefits and limitations on-farm, resulting in each genus being classified as: 'Desirable' and 'Undesirable' (Table S1). The categorization per tree genera was cross-referenced with all the citing sources. When cross-referencing showed opposite categories, the final classification was based on the highest number of citing sources.

The shade tree genera list was cross-referenced with the Taxonomic Name Resolution Service v. 4.0 (Boyle et al., 2013), to correct inconsistencies and remove synonyms. We then used Phylomatic to construct a phylogeny of all taxa based on the megatree of Zanne et al. (2014). Due to the absence of identification of *Cocos* and *Elaeis* genera in this database, information for these two taxa were entered at the species level (*Cocos nucifera* and *Elaeis guineensis*, respectively; Table S1). Phylogenetic trees were plotted with {picante} R package, for the global database and by country of study. Faith's Index, corresponding to the sum of length of all branches, was calculated for all the plotted phylogenetic trees. Phylogenetic distance between each shade tree genera and *T. cacao* was calculated with the *cophenetic* function. The average distances between 'Desirable' and 'Undesirable' classified shade tree genera and *T. cacao* as well as the average distance between genera in each shade tree 'use' subcategory and *T. cacao* were compared using an Analysis of Variance with a type III error using the {car} R package.

**3. Results and Discussion**

Despite the growing market demand for sustainably produced cocoa and the call for pro-environmental cocoa management (Asare and Anders, 2016), broad, theory-driven assessments of shade tree selection remain largely underrepresented. We categorized 78 shade tree genera across four of the main cocoa producing countries in sub-Saharan Africa: Ghana, Cameroon, Ivory Coast and Nigeria (Table S1). Among this list, 52 genera were classified as 'Desirable' and 26 as 'Undesirable'. Shade tree desirability is first and foremost based on the quality of the shade provided (Asare, 2005), pest regulation (Andres et al., 2018), soil health enhancement and resource use complementarity (Isaac and Borden,



**Fig. 2**

Fig. 2. Phylogenetic tree of the shade tree genera in *Theobroma cacao* (cocoa) agroforestry systems in (a) Ghana, (b) Cameroon, (c) Ivory Coast, and (d) Nigeria. Shade tree genera classified as desirable are in green, and shade tree genera classified as undesirable are in red. Tip edge shape indicates the dominant shade tree use (circle = food crops; triangle = timber; cross = other). Total number of shade tree genera, Faith's index and shade tree genera dissimilarity with *T. cacao* between desired and undesired genera are also provided.

2019), and the production of goods and materials (Somarriba and López Sampson, 2018). And indeed, classification of tree desirability was overwhelmingly in agreement through our study findings (81% of the identified genera had an all-desirable or all-undesirable rating) and between the four studied countries (Table S1).

As hypothesized, phylogenetic distance between shade tree genera and *T. cacao* was higher for the desirable shade tree genera both at the subcontinental (F-value = 5.60, p-value = 0.02) (Fig. 1) and national (Fig. 2) level. Phylogenetic diversity has been shown to explain a suite of ecosystem functions based on a higher likelihood of niche differentiation (Cadotte et al., 2012; Srivastava et al., 2012), with taxonomic divergence reported to limit competition for water and nutrient resources in cocoa agroforestry systems (Isaac et al., 2014; Niether et al., 2019). In fact, opposing resource acquisition strategies have been exposed in

optimal shade tree and crop pairings (Isaac and Borden, 2019).

While no plant functional traits were tested in our study, trees with low phylogenetic distance with *T. cacao*, such as *Cola* and *Ceiba* spp, were classified as undesirable because of their well-established propagation of cocoa pests (Asare, 2005). At a broader scale, tree genera from the same evolutionary node often shared the same classification. For instance, *Garcinia* spp, *Irvingia* spp, *Ricinodendron* spp and *Hevea* spp derived from the same node, were all perceived as desirable genera (Fig. 1). Shade trees with high phylogenetic distance were clustered together on the phylogenetic tree, and included *Albizia* and *Acacia* spp, well known N<sub>2</sub> fixing taxa that contribute extensively to soil fertility. These two principles, resource complementarity and pest and disease suppression, repeatedly appear as two strong criteria for shade tree desirability (Asare, 2005; Andres et al., 2018). The provisioning of goods

and materials, such as timber, fruit and medicine, for the local community is also a well-documented desirable trait of shade trees, given the significant contribution to farmers' financial stability (Somarriba and López Sampson, 2018). We report 77% of shade trees that provide food (e.g. *Persea spp*) were categorized as desirable, in contrast to 65% for timber shade trees and only 52% for the shade trees with other uses (Table S1), and indeed, evolutionary distance between *T. cacao* and shade trees within each of these sub-groups significantly differed (F-value = 3.86, p-value = 0.03).

A contemporary obstacle to the establishment of widely applicable recommendations of suitable shade tree taxa is the barrier to linking tree taxonomy to on-farm function. Our results show that phylogenetic distance could be a useful tool to predict a taxon's *a priori* suitability in cocoa agroforests. While further research is needed to confirm this application, our trends suggest that new shade tree genera recommendations could be made based on their evolutionary distance to *T. cacao*, a measure more easily obtained than, for instance, rooting structure, resource demand or, broadly, functional trait syndromes. This approach is transferable to other dominant tree-crops globally, such as coffee (*Coffea arabica*) and tea (*Camellia sinensis*), and thus provides a framework for generalizable but locally applicable and genera-specific recommendations. Next steps include testing whether phylogenetic distance is linked to a specific desirability criterion, such as pest propagation, or competition with light, water or soil nutrient resources. Linking plant functional traits, which has currently been measured for a relatively low number of species, to their evolutionary distance would further support the phylogenetic-based selection of new shade tree taxa. While national and subnational recommendations for shade tree selection are well developed, institutes, development practitioners, extension agencies and researchers could benefit from a more precise and theory-based shade tree advice tool for agroforestry systems.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.107125>.

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