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REVIEW ARTICLE

Functional complementarity: a review and a new methodological protocol applied to agroforestry systems

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Urgent ecosystem restoration is needed in a world with increasing food demands and 80% of agricultural lands degraded. Agroforestry systems (hereafter AFS), which integrate trees and crops, offer a potential solution for ecosystem restoration while providing food resources. The application of the functional trait approach is increasingly recognized for developing resilient and sustainable human-designed ecosystems, particularly through the application of functional complementarity (FC) theory. Then, an enhanced understanding of how FC operates in the context of AFS restoration efforts can help to reverse land degradation and foster sustainable land management. This study provides an in-depth review of the field of FC in restoration. Beyond summarizing the progression from theory to practical applications, our review highlights the necessity for additional criteria in selecting plant species and assemblages based on FC, especially for productive restoration. To fill this gap, we introduce a novel multicriteria protocol designed to assist in selecting assemblages with varying levels of FC, focusing on AFS in the humid tropics. The protocol systematically identifies species suitable for constructing these assemblages, giving priority based on local knowledge and community involvement while considering several methodological and technical challenges. We exemplified the use of the protocol through a case study from southeastern Mexico. Offering a comprehensive approach, our protocol aims to advance the application of FC in restoring productive systems by integrating ecological, technical, and social considerations in species and assemblages selection.

Key words: agroforestry systems, Lacandon rainforest, México, multicriteria assemblage selection, productive restoration, trait-based species selection

Implications for Practice

- Using complementary functional traits for selecting plant species and assemblages could improve the performance of productive restoration.
- A new protocol for selecting and prioritizing species and assemblages for productive restoration within agroforestry systems is provided.
- The protocol guides the assembly of species groups with different functional complementarity levels.
- The protocol integrates societal, ecological, and technical criteria, aligning with local needs and potentially improving project success.
- Implementing the protocol in the field raised recommendations and revealed challenges in its application.

Introduction

The increasing global demand for food, fueled by population growth (UN 2022), presents significant challenges for biodiversity conservation. Worldwide, 80% of agricultural land is degraded, leading to expansion into new areas and causing the loss of natural ecosystems and their contributions to people (IPBES 2018). As a result, there is a growing urgency to restore ecosystems (Laughlin 2014). Ecosystem restoration (ER) involves assisting the recovery of degraded or destroyed ecosystems through various methods (UN 2024). One approach

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is productive restoration, which combines reestablishing original ecosystem elements with agroecological or agroforestry management, providing goods and services to local communities (Ceccon 2013).

Agroforestry systems (AFS) offer a potentially sustainable approach in areas inhabited by humans (Minnemeyer et al. 2011). These systems combine trees with crops, allowing the recovery of ecosystem properties while providing food resources to improve human livelihoods (Montagnini & Metzel 2017). About 74% (1.5 billion over 2 billion hectares) of restorable global land is suitable for establishing land use mosaics, including agroforestry (Minnemeyer et al. 2011). This figure is higher in tropical regions, highlighting the value of agroforestry for restoration efforts in these regions.

Functional restoration is emerging as a prominent perspective on restoration (Cadotte et al. 2011; Wang et al. 2020). This approach focuses on creating resilient and enduring ecosystems that can adapt to the social-ecological changes associated with global change (Jacobs et al. 2015; Reid 2018). Furthermore, functional restoration promotes the provision and maintenance of ecosystem processes (Laughlin 2014; Ostertag et al. 2015).

Functional restoration approaches analyze biotic communities and ecosystems based on functional traits (Díaz et al. 2007). *Functional traits* are measurable morphological, physiological, or behavioral attributes of organisms that impact their fitness (survival, growth, and reproduction) or influence ecosystem functioning (Lavorel & Garnier 2002; Violle et al. 2007) and services (Díaz et al. 2007). In trait-based approaches, although continuous traits (e.g. specific leaf area and wood density) are commonly used, categorical functional traits that could be used as functional groups (e.g. life form, dispersal mode, and photosynthesis type) are also applied (Mason et al. 2005; Díaz et al. 2007). The link between species' functional traits and their responses to environmental changes, or their roles in ecological processes, is well established (Lavorel & Garnier 2002). The selection of traits should align with the specific aims and conditions of each restoration project (Loureiro et al. 2023).

Within a plant assemblage, species exhibit varying trait values, representing the diversity of functional resource acquisition strategies and their responses to environmental changes (Lavorel et al. 1997). The kinds, quantities, relative abundances, and distribution of functional traits within an assemblage collectively define its *functional diversity*, which can be quantitatively assessed (Mason et al. 2005; Díaz et al. 2007).

Functional diversity comprises three main components: functional richness (FR), functional divergence (FD), and functional evenness (FE; Mason & Mouillot 2013), which describe the distribution of trait values and their abundances within an n-dimensional functional space (Petchey & Gaston, 2006). FE, which measures the regularity of trait values and abundances across this space, is key to ecosystem functioning, such as productivity, by indicating differential resource use among species (Mason et al. 2005). Thus, FE is commonly related to *functional complementarity* (FC), a mechanism that promotes species coexistence through niche differentiation, where species with distinct traits maximize resource capture and use, purportedly enhancing ecosystem productivity (Tilman et al. 2014). The FE–FC relationship is positive in environments where resources are abundant and homogeneously distributed in space (Mouillot et al. 2005). However, in ecosystems with uneven resource distribution, other mechanisms—such as the dominance of key trait species—may be more related to productivity than FC (Petchey 2004; Hooper et al. 2005).

A meta-analysis by van der Plas et al. (2020) found that functional trait dissimilarity explained only 33% of ecosystem functions in grasslands with herb and grass species rather than in restoration contexts. Other studies indicate that complementary species strategies increase productivity in both grassland and forest ecosystems (Zheng et al. 2024). Further research is needed to evaluate FC's role in restoration, especially where plant species vary widely in life forms, as in AFS.

FC is a valuable approach to restoration, allowing the reassembly of functional traits to meet specific goals. Some studies have used trait-based restoration, assembling species with complementary traits to enhance ecosystem productivity or control invasive species (Funk et al. 2008; Laughlin 2014). This approach highlights the importance of functional traits and their interactions, supporting more targeted and effective restoration strategies.

In restoration, challenges arise in species selection and reassembly, which can be addressed by incorporating FC. While trait-based restoration is an evolving field (Wang et al. 2021), it holds particular promise in AFS, where further research is essential to deepen our understanding of FC and its integration into their functioning. Applying functional restoration in AFS has the potential to reverse land degradation and encourage sustainable land management practices (IPBES 2018).

This study has two main objectives. First, we perform a systematic literature review on FC in the context of restoration, documenting theoretical or applied advancements. While functional diversity and ecosystem functioning are well documented (Ali 2023), comprehensive reviews on the potential role of plant functional diversity—especially FC—in restoration are still lacking.

Second, we introduce a novel protocol for identifying and selecting functionally complementary plant species and assemblages, especially useful for productive restoration using AFS in areas with high plant species diversity, such as the humid tropical region. Lastly, we exemplified the use of the protocol in a case study from southeast Mexico.

Methods

Literature Review

We conducted a systematic literature search to identify relevant papers on FC in restoration. Based on the ISI Web of Knowledge database, we used a search equation with keywords related to restoration, community assembly, and FC. Finally, we selected those studies addressing FC from a theoretical or applied perspective. Details are in Supplement S1.

Using the selected papers, we provided a chronological overview of the development of the FC field. Furthermore, we classified each study according to its type—theoretical, a blend of

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theory and application, or applied research—and assessed the contributions of theoretical advances and their implementation. Finally, we described research trends considering the study systems of selected papers.

Protocol for Selecting Assemblages With Contrast Levels of Functional Complementarity

We propose a multicriteria protocol for restoration using AFS and FC to select species and assemblages. The protocol is designed for highly biodiverse humid tropical regions but could also be applicable in other areas with high species diversity. This protocol encompasses three main steps: (1) species selection, (2) formation of assemblages based on FC, and (3) assemblage selection (Fig. 1).

Species Selection. *Recognizing Useful Species.* First, for a given region, herbaceous, shrub, and tree species, cultivated or native, with commercial or practical value, are identified based on local knowledge, literature, and electronic databases (e.g. governmental reports).

Identifying Potential Species. The resulting species list is filtered to isolate those that can be easily propagated at the target site.

Validation of Potential Species. The list of selected species is validated through field surveys in collaboration with local people with experience in agricultural or forest management. The surveys aim to acquire local knowledge regarding the ease of propagating and cultivating species, their value to the local population, and to gather information, such as the availability of parent plants, among other details. To streamline this process, identification tools (e.g. an illustrated species catalog) should be utilized to ensure accurate identification of viable species among stakeholders (Fig. 1).

Database Construction. For the viable species, all relevant information regarding their uses (people's interest or value), ecological attributes (e.g. origin, life-form, nitrogen-fixing capacity, and fruiting seasons), technical information about propagation and cultivation, along with functional traits, is included in a database.

For AFS, the selection of functional traits should reflect the species' ability to use essential resources, such as water, light, and nutrients (e.g. height, specific leaf area, and wood density), and their potential competitiveness for these resources. Moreover, functional traits aligned with specific restoration aims and environmental conditions could be selected. Functional trait values can be obtained from field measurements (Pérez-Harguindeguy et al. 2013) or electronic databases such as BIEN (Maitner et al. 2017). Assuming phylogenetic conservatism of functional traits (Ackerly 2009), when specific trait values for a species are unavailable, average values from the genus or nearest taxonomic level may be employed.

Assemblages Based on Functional Complementarity *Creation of Assemblages.* Stratified random assemblages are constructed by combining a desired number of herb, shrub, and tree species selected from a list of viable species (Fig. 1). Initially, viable species are categorized by life form or other desired attributes, ensuring each category includes as many species as possible. A general assemblage composition for AFS might include species in these social-ecological categories: long-lived native timber species (TS), fast-growing native tree, shrub, or non-annual crop service species (SS), and annual commercial species (CS; Beer et al. 2003). The type and number of categories may vary based on the objectives of the restoration project.

One or more species are randomly selected from the species pool of each category to create diverse assemblages. The selection process can be performed using a randomized routine in R or other platforms. It is recommended to generate as many random assemblages as possible, considering the number of species available, to ensure a wide range of combinations. The number of random assemblages depends on the species pool size per category and can be calculated using the rule of product in combinatorics (Rosen 2011) as TS × SS × CS. For example, with 10 species per TS, SS, CS category, up to 1000 assemblages are possible. Combinations increase exponentially with more species but decrease from 125 (five species per category) to eight (two species per category) with fewer species. Thus, it is recommended to have at least five species per category.

Estimation of Functional Complementarity. A FC value is calculated for each generated assemblage. Different indicators of FC are available in the literature (Schleuter et al. 2010). We suggest using (modified functional attribute diversity [MFAD]) when species abundance data is unknown.

To calculate MFAD, first, the functional dissimilitude between all pairs of species in the assemblage was obtained (Marczewski-Steinhaus index; Podani 2000):

$$d_{hk} = \frac{\sum_{i=1}^{p} |a_{hi} - a_{ki}|}{\sum_{i=1}^{p} \max\{a_{hi}, a_{ki}\}}$$

Here, a_{hi} is the value of a functional trait i for species h, and a_{ki} is the same trait value for species k. "Species" refers to functional species that differ in their functional trait values (i.e. two or more taxonomical species with identical trait values are a functional species). The absolute difference between pairwise trait values is calculated from trait one to trait p. The denominator sums the maximum values among all species pairs for each trait. Then, the following formula is used:

$$\text{MFAD} = \frac{\sum_{h=1}^{N} \sum_{k=1}^{N} d_{hk}}{n}$$

Here, d_{hk} is the sum of dissimilarities across all traits between species h and k, and n is the number of species in the assemblage. Finally, MFAD is obtained by summing all dissimilitude values calculated for each functional species and dividing by the total number of functional species (Schmera et al. 2009). MFAD

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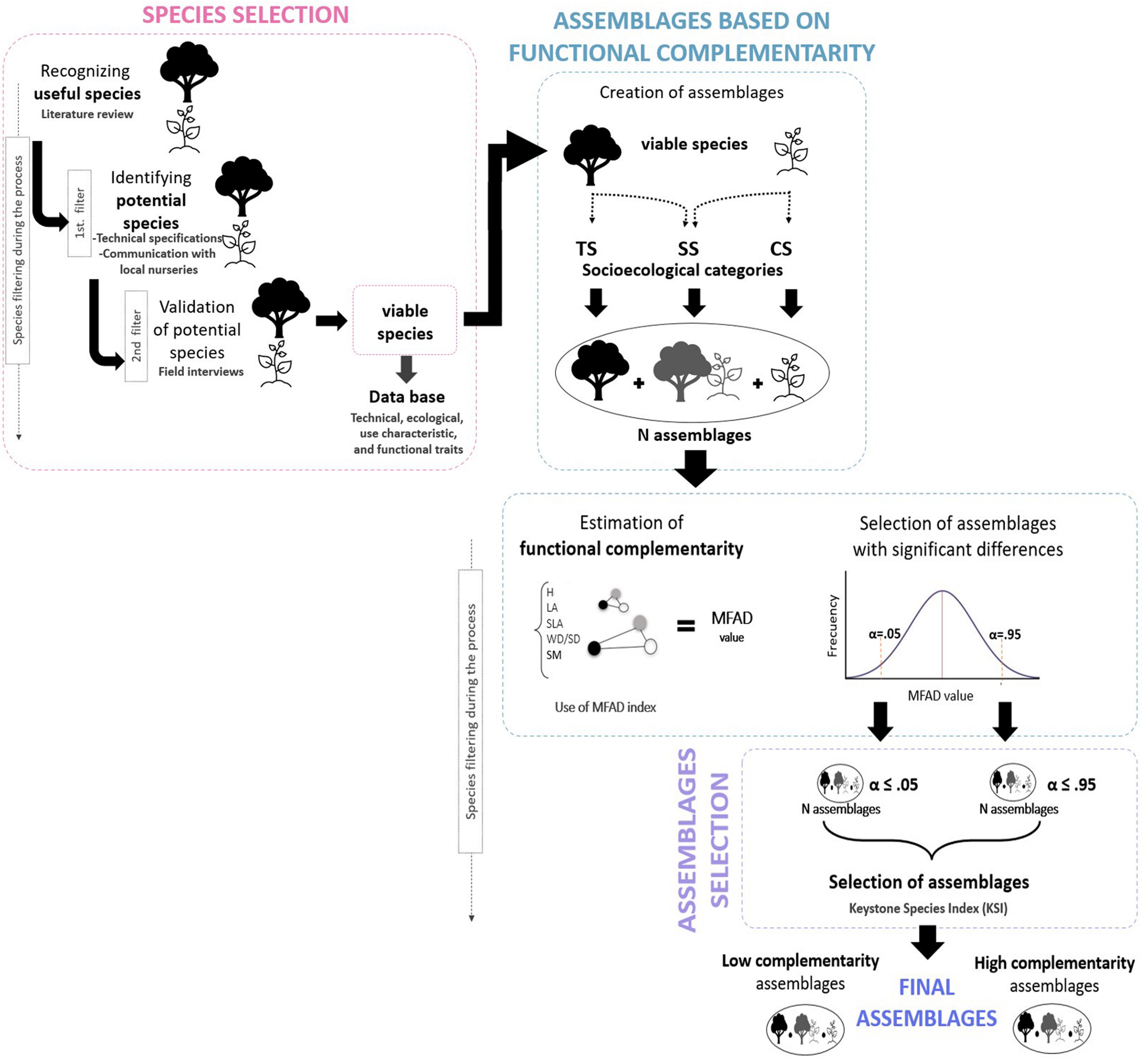

Figure 1. A scheme of the multicriteria protocol is proposed for selecting species and assemblages suitable for restoration using agroforestry systems based on functional complementarity. The main steps are depicted in color text. Within each step, different activities are shown. The methods used are presented in small text, and the main results for each step are highlighted in bold. The tree symbol represents tree species, while the herb symbol represents crops. The ellipses with tree and herb symbols represent the assemblages. Socioecological categories: timber species (TS), service species (SS), and commercial value species (CS).

ranges from 0 to 1, with higher values indicating greater functional regularity or complementarity.

Selecting assemblages with higher functional complementarity. After calculating the FC values for all generated assemblages, values are arranged in increasing order. A criterion is then established to identify assemblages with high complementarity. It is recommended to select assemblages in the top 5% for high complementarity, similar to a p value of 0.05 or lower. Likewise, the lowest 5% represents assemblages with the least complementarity.

Assemblage Selection. Finally, the selection of assemblages should prioritize those that align with specific restoration aims, consider the availability of propagules, and cater to the interests of local users, among other aspects. To facilitate this prioritization process, we created a Key Species Index (KSI) that ranks the social-ecological suitability of species for restoration with AFS. In this way, the final selection includes the most suitable assemblages based on the quantitative dissimilarity of functional traits (through MFAD) and the socioecological

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variables applied via the KSI, resulting in a comprehensive selection. The selection process is illustrated in the following case study.

Case Study

To illustrate the protocol's use, we identified plant species that are potentially viable and are of priority in the study site for creating complementary assemblages in the initial stage of AFS.

Following the protocol, we compiled a list of tree, herbaceous, and shrub species with utilitarian value from the Lacandon region (Supplement S2). The lists were obtained from literature sources, interviews, and workshops conducted with local communities. The species' ecological attributes and propagation methods were sourced from literature and local nurseries.

From the generated list, we selected tree and shrub species with the potential to be propagated in the region and crop species well-suited for establishing AFS. Crop species with a climbing habit and those used for cultivating tubers or roots were excluded (Beer et al. 2003). Also, we only considered species with available propagules for initiating restoration activities during a specific season, autumn, since it is the rainy season. This initial filter (Fig. 1) gave us a list of potential species suitable for restoration within AFS.

We conducted 14 interviews with farmers and individuals with forest knowledge to validate the list of potential species. During these interviews, we used an illustrated catalog of the potential species to gather insights into their familiarity with the species, usage, propagation methods, and their interest in cultivating them. The interviews also provided information on cultivation practices, prevalent diseases, and locations where the plants thrive, among other insights (Fig. 1). Based on this information, we narrowed our selection to the viable species, choosing those that could actually be propagated on-site. However, during the species and assemblage selection process, the pool of viable species gradually decreased, primarily due to the constraints imposed by suitable propagation timelines.

The narrowed-down list of viable species was used in the subsequent steps of the protocol (Fig. 1). For these species, we compiled a database including information on uses, technical and ecological attributes, and functional traits pertinent to restoration using AFS. We opted for ecologically significant functional traits associated with species survival, growth, and/or reproduction, which contribute to the species' fitness (Lavorel et al. 2007; Garnier & Navas 2012) and are easy to measure (Díaz et al. 2004). The selected traits and their relevance to plant function are shown in Table 1. Values for these traits were derived from earlier studies carried out in our study region (Tauro 2013; Lohbeck 2014; Rodriguez-Cedillo 2014) and from the BIEN open database (Maitner et al. 2018).

Using the database information, we generated random assemblages. Each assemblage consisted of one species from each of the social-ecological interest categories: (1) native long-lived timber tree species (TS group), (2) non-annual herbaceous crop species or native fast-growing tree or one shrub species with ecological (e.g. nitrogen fixer) or productive (e.g. leaves, fruits, seeds) services (SS group), and (3) annual crop species with commercial value (CS group, Fig. 1). For each assemblage, we calculated a FC value using the MFAD index. Then, assemblages with low complementarity ($p = 0.05$, MFAD ≤0.50) and assemblages with high complementarity ($p = 0.95$, MFAD ≥0.89) were selected.

Table 1. Functional traits used and plant functions related.

Functional trait	*Plant function related*	*References*
Height (H, m)	Competitive ability, light acquisition, and vertical position	Garnier and Navas (2012)
Leaf area (LA; cm^2)	Light interception and water balance	Díaz et al. (2016)
Specific leaf area (SLA; cm^3/g)	Relative growth rate, photosynthetic capacity, related to primary productivity and resource economy	Reich et al. (1997); Poorter and Bongers (2006); Garnier and Navas (2012)
Wood and stem density (WD, SD; g/cm^3)	Defense properties, mechanical damage; storage and hydraulic capacity	Chave et al. (2009); Pérez-Harguindeguy et al. (2013)
Seed mass (SM; mg)	Dispersal distance, seed germination and seedling establishment, related to establishment success	Moles and Westoby (2006); Westoby et al. (2002); Pérez-Harguindeguy et al. (2013)

To select assemblages, we prioritized assemblages with species whose propagules could be easily obtained and meet the socioecological objectives of productive restoration. We developed a KSI to facilitate prioritization. KSI condenses the species' viability, considering technical criteria, usage importance, and ecological factors. The KSI was calculated as the sum of seven indicators, each ranging from 0 to 1. Higher KSI values indicate an increasing capability of the species to meet the socioecological objectives of productive restoration.

After completing the selection process, we selected six assemblages: three with low complementarity and three with high complementarity. We are conducting a long-term field experiment (>3 years) to determine whether these contrasting complementarity groups exhibit differences in species performance and productivity (seed, fruit, or timber production). The results of the experiment will be presented in a separate paper.

Results and Discussion

Literature Review

Our review retrieved 63,633 papers published in English or Spanish linked with biology, forestry, environmental sciences, agronomy, and physiology. We selected the most cited articles to focus on fundamental advances in restoration using FC,

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resulting in a subset of 402 papers. Afterward, we focused on research studies concerning plants or vegetation, resulting in 76 papers (from ISI WoS) and 59 from secondary sources (Table S1). A detailed read of these papers allowed us to identify 16 studies explicitly addressing issues of FC, with some focusing on restoration (Table S2). The following discussion is based on these papers.

Research over Time. Our review showed that the study and application of FC in restoration still need to be improved. Except for Funk et al. (2008), most of the research was initiated after 2010, with an increase from 2015 onwards (Fig. 2). Between 2013 and 2015, studies mainly focused on theoretical issues and synthesis, but afterward, the link between functional diversity and ecosystem services was approached (Fig. 2; e.g. Häger & Avalos 2017; Williams et al. 2017). The transition from theory to application (Funk et al. 2008) in restoration has taken place since the end of the twentieth century following the foundational studies on the functional trait approach, such as the standardization of the functional trait term (Violle et al. 2007), and the pioneering experiments on FC (Tilman et al. 1997). This progress continued and led to the development of digital tools for species selection for restoration (e.g. Laughlin et al. 2018). Such progress has come to integrate functional trait principles into restoration practices, even in collaborative projects with government entities (e.g. Rayome et al. 2019).

Advances in Trait-Based Restoration and Functional Complementarity. The study of FC has contributed to restoration theory and practice. Our review identified two theoretical studies, four linking theory and application, and 10 strictly applied research studies (Fig. 3).

Theoretical Development. In the theoretical area, it was argued that FC is key in stabilizing ecosystems (Loreau & Mazancourt 2013). Furthermore, research on functional traits is increasing, yet only 12% of restoration studies use them a priori. In this context, complementarity appears to be a viable approach for functional restoration to enhance ecosystem services in tropical ecosystems (Carlucci et al. 2020). Additionally, it was recognized that species' efficiency in resource utilization, resource availability, and multiple environmental abiotic conditions influence the effect of complementarity on ecosystem processes (Hooper et al. 2005). Therefore, understanding how these dynamics influencing FC in different

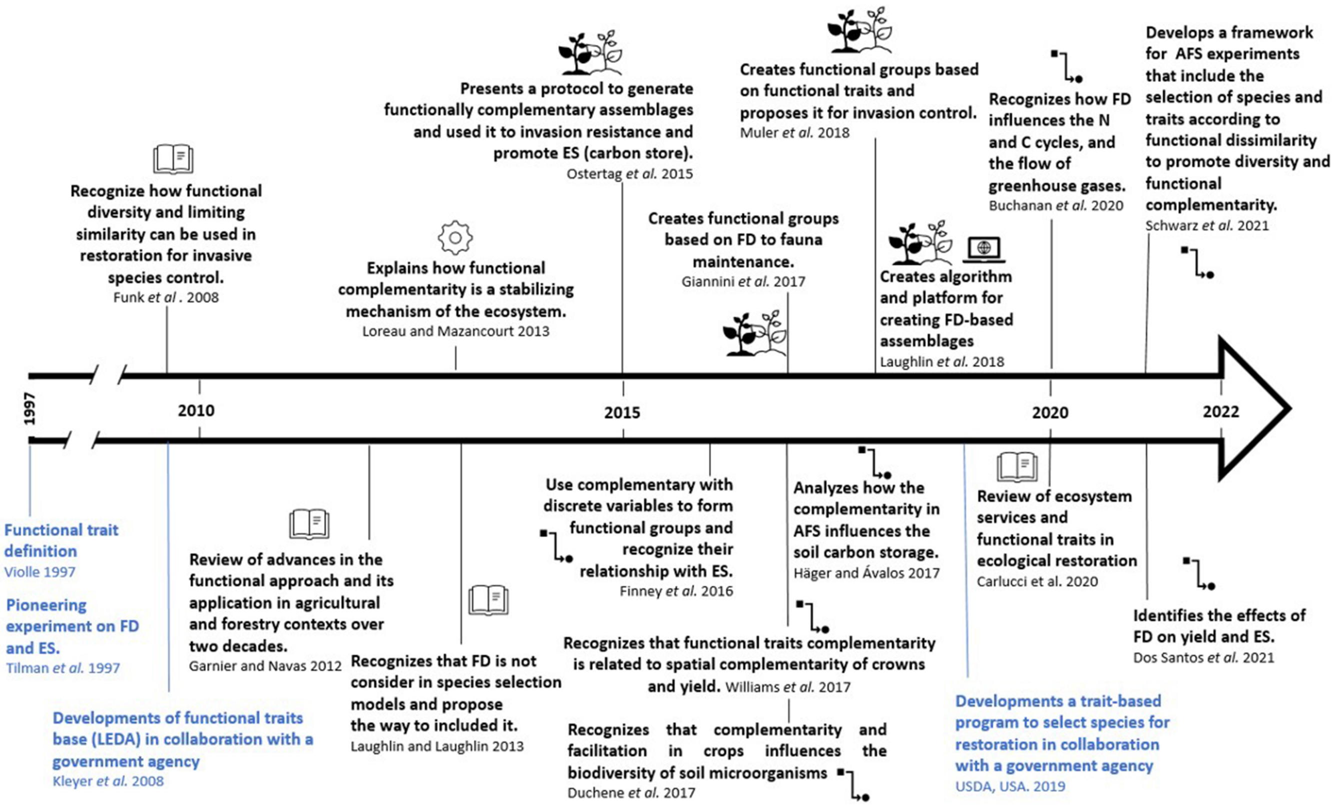

Figure 2. Timeline (1997–2022) of research development providing conceptual bases for functional complementarity in restoration with markers every 5 years. Each entry represents an article, and the legend summarizes the study's contribution. The symbols along the timeline represent different types of contributions: books for theoretical contributions, gears for ecological mechanisms, plants for species selection, connections for functional diversity linkage with ecosystem services, and computers for developing digital tools. The entries in blue denote relevant events of reference in the topic. AFS, agroforestry systems; C, carbon; ES, ecosystem services; FD, functional diversity; N, nitrogen.

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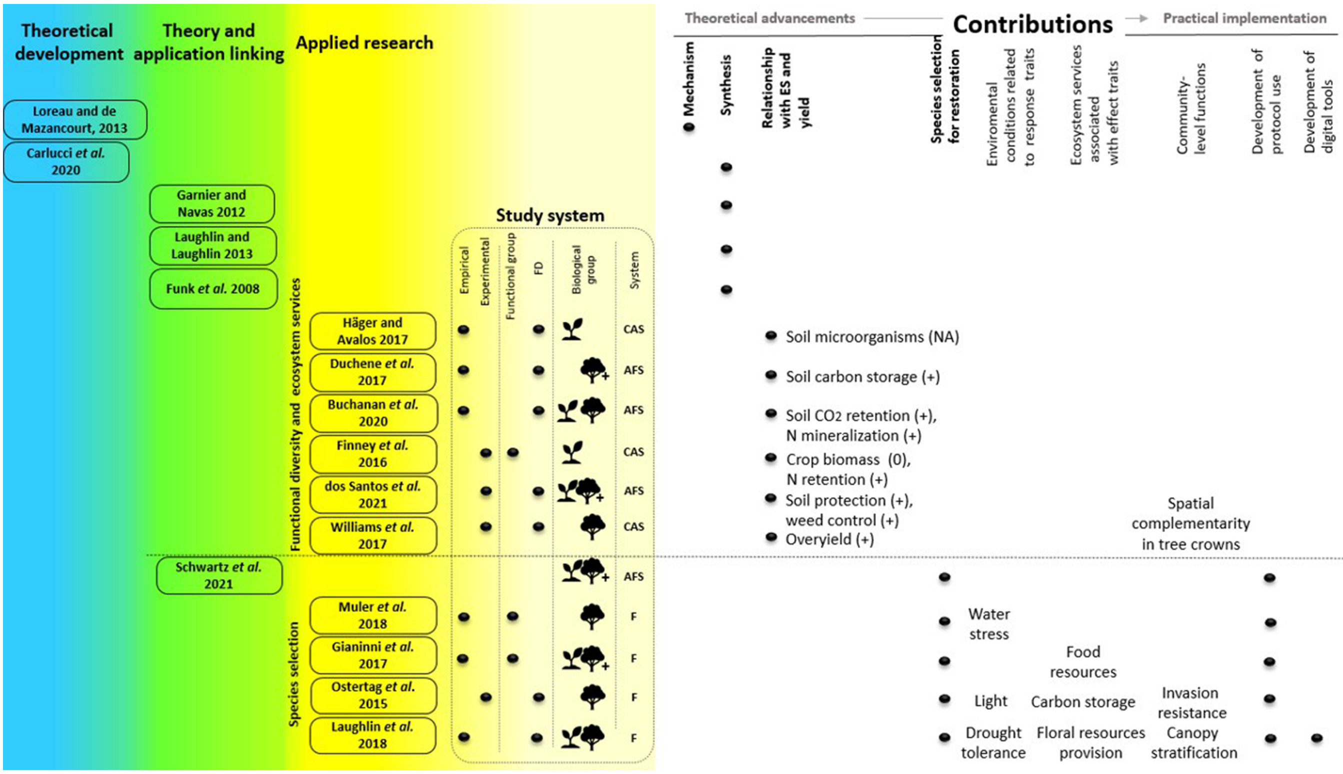

Figure 3. Theoretical and applied studies relevant for functional complementarity and trait-based restoration. From left to right, theoretical articles (deep blue), studies linking theory and application (light blue), and applied research articles (yellow). Reference papers are within rounded rectangles. The applied research studies are divided into articles that relate functional diversity (FD) to ecosystem services and those focused on species selection. The study system section summarizes the type of research (empirical or experimental), the type of FD estimation method used (functional group or FD with continuous variables), the biological groups studied (herb symbol: crop, tree symbol: tree, plus sign: other life forms), and the system where the study was conducted (AFS, agroforestry systems; CAS, cropland-agricultural systems; F, forest). In the white area, the studies' contributions are presented on a gradient from theory to application: explanation of biological mechanisms, synthesis of knowledge, the relationship between FD and ecosystem services and performance, specifying the type of ecosystem service. The dark point signifies that the study contributes to that aspect. the paragraphs specify the kind of ecosystem service. The symbol at the end of each variable indicates its relationship with FD (positive, +; neutral, 0; not applicable, NA). In studies about species selection, the paragraphs specify the environmental conditions associated with response traits, the ecosystem services associated with effect traits, and the functions related to community processes. Finally, tools such as usage protocols and digital tools are created.

ecosystems (Adler et al. 2013) could enhance the use of FC for restoration.

Linking Theory to Application. Our review identified four studies bounding theory with applied issues (Fig. 3). From 1990 to 2010, there was a clear trend toward adopting a functional approach in agriculture and forestry (Garnier & Navas 2012). Additionally, the importance of developing a species selection model for restoration grounded in the limiting similarity theory and its subsequent implementation was highlighted (Laughlin & Laughlin 2013). Also, the application of limiting similarity theory and functional diversity in restoration, particularly for managing invasive species, was noted (Funk et al. 2008). Finally, a framework for experimental design was proposed, encompassing criteria for species selection to foster FC in productive restoration (Fig. 3; Schwarz et al. 2021).

Applied Research. Among the 10 studies on applied research, six articles explored the relationship between functional diversity and ecosystem services or yield production. In these studies, nearly 70% of the response variables (e.g. soil carbon storage and overyield) showed a positive relationship with functional diversity (Fig. 3).

Four studies focused on using functional traits for species selection in restoration (Fig. 3). Some studies centered on selecting species to address challenging environmental conditions, such as water stress exacerbated by climate change (e.g. Muler et al. 2018). Others aimed to improve ecosystem services by selecting species that provide resources for wildlife (e.g. Giannini et al. 2017), or to control invasive species (e.g. Ostertag et al. 2015). All these studies crafted protocols useful for stakeholders involved in restoration efforts. Additionally, a digital platform was developed to generate species assemblages (Laughlin et al. 2018).

In theory, functional traits operate in the "response" and "effect" dimensions (Lavorel & Garnier 2002). Proposals exist for both dimensions, with studies aimed at selecting species to respond to environmental conditions, such as drought (e.g. Muler et al. 2018), and proposals that promote ecosystem services, such as fauna maintenance, in the effect dimension

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(e.g. Giannini et al. 2017). Additionally, research focuses on reassembling plant communities to promote functions such as controlling invasive species (e.g. Fig. 3; Funk et al. 2008).

Beyond the findings of the reviewed studies, other advancements were recognized in the field. Alternative methodologies for species selection are emerging, such as identifying species by their functional similarity to target species, which show positive survival outcomes (Wang et al. 2020). Additionally, a collaborative platform with government entities has emerged, simplifying the process for users by predefining restoration goals and associated functional traits (Rayome et al. 2019). Furthermore, efforts are being made to make the application of functional traits more accessible in the field by establishing connections between their empirical use and scientific references, and by the development of citizen science plant trait initiatives (Isaac et al. 2018; Isaac & Martin 2019).

Another notable advancement is the existence of diverse public databases on functional traits, like Botanical Information and Ecology Network Database (RBIEN) or the TRY plant trait database (Maitner et al. 2018; Kattge et al. 2020), overcoming what was considered a challenge a decade ago (Garnier & Navas 2012). In this realm of tools, collaborations with governmental bodies have also been initiated (Kleyer et al. 2008). Such collaborations with stakeholders beyond academia are notable, as their participation can catalyze the adoption of functional ecology among a broader community of restoration practitioners (Merchant et al. 2022).

Based on the above, it is evident that validated frameworks are being developed through experimental studies (e.g. Ostertag et al. 2015; Carlucci et al. 2020; Wang et al. 2020), as well as adaptations that enhance species selection by refining methods (e.g. Laughlin et al. 2018), while also facilitating both the selection and accessibility of functional traits. Progress is also being made in improving accessibility (e.g. Rayome et al. 2019) and adaptability to different contexts. These advancements address challenges associated with applying functional approaches in restoration practice (Carlucci et al. 2020; Merchant et al. 2022). The progression toward more user-friendly interfaces or mobile applications could be the next step in improving tool accessibility for a broader audience.

However, despite progress in selecting assemblages issues (Laughlin et al. 2018; Wang et al. 2021), knowledge and implementation gaps remain, necessitating concentrated efforts to improve the understanding, efficiency, and applicability of functional restoration practices. For instance, assemblage selection has been oriented toward ecological restoration (Ostertag et al. 2015; Laughlin et al. 2018; Carlucci et al. 2020), while FC in AFS has only been partially addressed (Schwarz et al. 2021).

Study Systems and Methods. Regarding studies using FC in restoration, we recorded one conceptual, six empirical, and four experimental studies (Fig. 3). In these, functional diversity (which is positively related to FC) was quantified using continuous metrics or functional groups (Table S2; Fig. 3). Most studies utilized continuous metrics, which offer improved discrimination among species assemblages compared to functional groups (Schleuter et al. 2010). The studies used a wide variety of metrics, highlighting the diverse range of species selection methods used in restoration, as was also noted by Wang et al. (2021).

Different functional diversity metrics exhibit varying precision levels (Schleuter et al. 2010) and sensitivities to changes in species abundance and trait dissimilarity within assemblages (Bello et al. 2013; McPherson et al. 2018). Furthermore, each metric represents different dimensions of functional diversity through distinct algorithms (Schleuter et al. 2010), underlining the importance of evaluating the performance disparities among metrics when selecting species for restoration efforts.

In this sense, an important step in restoration based on functional diversity entails the selection of the metrics with the best performance. Such performance must align with each restoration project's objectives, the used plant assemblages, and the prevailing environmental context. For example, the metrics that are suitable for restoration projects using a wide trait variability, such as AFS (that combine contrasting life forms), could be different from those suitable for projects using a single life form with a narrow trait variability, such as when restoration considers only tree species. Elucidating and validating metrics with higher performance could streamline the metric selection process for other restoration practitioners needing to be more directly engaged with functional diversity metrics.

Historically, basic trait-based research was primarily conducted in grasslands (Garnier & Navas 2012). However, our review shows an expansion in the systems studied, now predominantly focusing on tree or woody species (Table S2; Fig. 3). Six of the 11 studies we detected included at least two plant life forms and eight woody species (trees, shrubs, or lianas). Additionally, there has been an increase in the variety of systems, including natural ecosystems, AFS, and agricultural systems (Table S2; Fig. 3). Also, to date, the global network of tree diversity research (TreeDivNet; http://www.treedivnet.ugent.be/index.html) has reported 16 studies on functional diversity across various ecosystems.

Our review underscores the growth and broadening of basic and applied trait-based research in restoration. This expansion has encompassed various life forms, natural ecosystems, and systems with human intervention. However, restoration involving AFS presents particular characteristics, as these systems integrate diverse life forms, species of practical importance, productive management practices, and the potential prioritization of some species over others. These multifaceted factors raise challenges that might curtail the transferability of trait-based research outcomes from natural ecosystems to AFS (Schwarz et al. 2021).

Protocol for Selecting Assemblages With Contrast Levels of Functional Complementarity

Species Selection. Following our protocol (see Section 2), we identified 206 species with useful value in the Lacandon region. A total of 141 tree species were included (Table S3), with 33 considered potentially helpful (first filter), though four were later excluded during field validation (second filter; Table S4) due to species misidentification or difficulties in their

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propagation, leaving 29 viable species (14% of the total of 206) suitable for restoration with AFS (Table S5). Nine of these were further excluded from the next steps due to the inability to obtain propagules (either because the seeds were inaccessible or the fruiting season had already concluded; Table S5).

For herbaceous and shrub species, 65 useful species were identified (Table S6). For this, 21 species were excluded in the first filter because they presented undesirable characteristics to establish a herbaceous layer in AFS (e.g. climbing habit or crops for cultivating tubers or roots; Table S7). Another 28 species were eliminated during field validation (second filter) because they were unknown in the region, were not cultivated, or the community was not interested in cultivating them (Table S7). Six more were excluded throughout the process due to the inability to obtain propagules as their fruiting season had already finished (Table S7).

We ended with 20 tree species (Table S5) and 10 herbaceous or shrub crop species (Table S8) for forming random assemblages suitable for initiating restoration with AFS. 14 tree species were assigned to the TS category, 12 fast-growing native tree, shrub, or non-annual crop SS to the SS category, and eight annual crop species to the CS category. Among the viable tree species, we included the most important tree species in local AFS according to the KSI: *Erythrina folkersii*, *Cojoba arborea*, *Dialium guianense*, *Inga pavoniana*, and *Brosimum alicastrum* (Table S5). Regarding crop species, we included *Capsicum annuum*, *Crotalaria longirostrata* (a nitrogen-fixing plant), and *Physalis philadelphica* due to high interest levels. We did not observe limitations in obtaining propagules for the most viable species in the region (Table S8).

Our protocol adopts a multi-criteria approach for species selection, encompassing functional traits, ecological factors, technical feasibility, and socio-economic considerations.

Incorporating functional traits enhances the identification of species best suited for achieving restoration goals, contrasting with previous protocols that lacked a functional perspective despite using multi-criteria selection (Meli et al. 2014). Some proposals, for example, limited their focus to selecting species based solely on functional traits (e.g. Muler et al. 2018), or mentioned the importance of pragmatic or logistical criteria but did not systematically integrate them (e.g. Ostertag et al. 2015). Our protocol stands out by its structured steps where various technical and socioecological criteria are considered in the species selection process. It offers a systematic approach to identifying viable species for restoration, especially when utilizing AFS.

An essential aspect of our species selection protocol is the integration of socio-economic factors, including identifying species used in local areas, the species' potential uses, and the species of interest for cultivation. Local people generated or confirmed all this information in the field. This entails community involvement in the species selection process and the restoration project itself (Hart 2013), potentially enhancing the acceptance and success of the project (Fox & Cundill 2018). In contrast, among the reviewed protocols, only two studies using functional trait approaches included societal variables, obtaining information from academics or literature (Giannini et al. 2017), with another study not specifying its information sources (e.g. Ostertag et al. 2015). Some other studies have addressed AFS' co-production and functional design processes (e.g. Hastings et al. 2020). Yet, they have not extensively covered the formation of assemblages and the nuances of FC.

Assemblage Formation and Selection. With the TF, SS, and CS species, we generated 1344 random assemblages. From these, we selected 67 with low complementarity (MFAD≤0.5) and 68 with high complementarity (MFAD ≥0.89), ensuring no species repetition occurred within the same assemblage. Also, we excluded assemblages with species whose propagules were unavailable during our experimental study (Table S9). Then, we prioritized those assemblages with the higher KSI species. Finally, six assemblages were selected, three with low (mean MFAD ±SE = 0.50 ± 0.01) and three with high complementarity (0.89 ± 0.01; Table 2). As expected, assemblages with high complementarity covered a larger functional space than those with low complementarity (Fig. 4). However, dissimilarity was not uniform across all functional traits. Height and wood density showed minimal dissimilarity differences between low and high complementarity assemblages, likely due to the inclusion of species with contrasting heights and wood densities across all assemblage types.

It is important to note that our protocol is best suited for systems with a relatively high number of species available

Table 2. Assemblages with contrasting levels of functional complementarity in the study case were identified using the protocol for species selection and assemblage. Each assemblage included one long-lived native timber species (TS), one fast-growing native tree, shrub, or nonannual crop service species (SS), and one annual commercial value species (CS).

Complementarity level	*TS*	*SS*	*CS*	*Acronym*
High	*Cedrela odorata* (Cedro)	*Crotalaria longirostrata* (Chipilín)	*Physalis philadelphica* (Tomate verde)	CQP
High	*Cedrela odorata* (Cedro)	*Bixa orellana* (Achiote)	*P. philadelphica* (Tomate verde)	CBP
High	*Tabebuia rosea* (Maculí)	*Ochroma pyramidale* (Balsa)	*Crotalaria longirostrata* (Chipilín)	TOQ
Low	*Cojoba arborea* (Frijolillo)	*Ananas comosus* (Piña)	*Capsicum annum* (Chile)	CoAK
Low	*Inga pavoniana* (Paterna)	*A. comosus* (Piña)	*C. annum* (Chile)	IAK
Low	*Brosimum alicastrum* (Ramón)	*Inga pavoniana* (Paterna)	*Lycopersicon esculentum* (Tomate rojo)	BrIL

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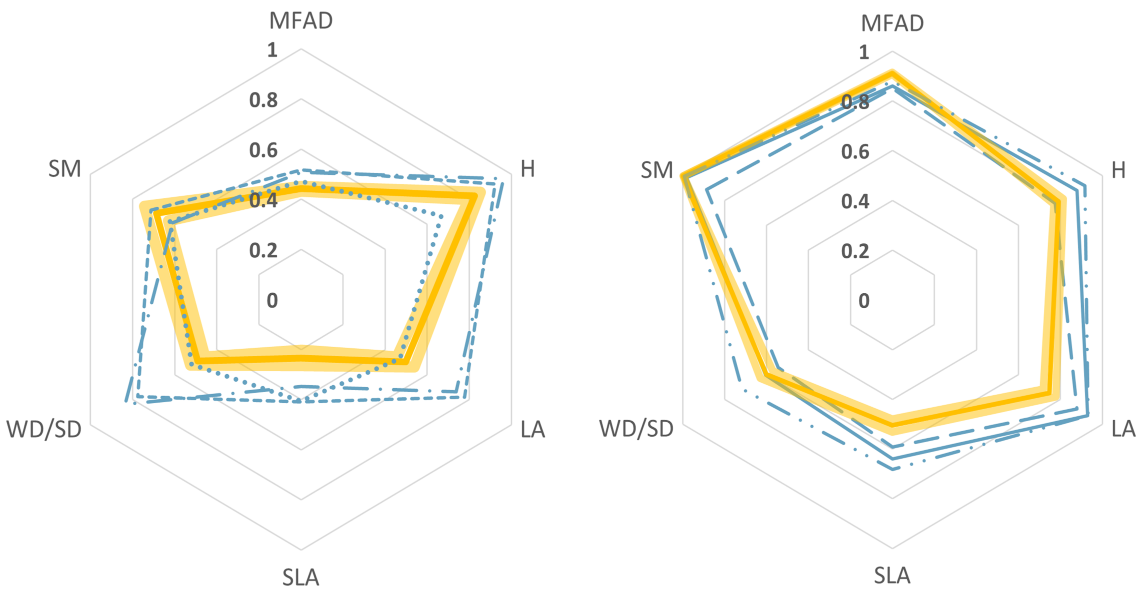

Figure 4. Radar chart diagram showing modified functional attribute diversity (MFAD) and dissimilarity values for five functional traits considered in the present study. Functional traits: H = height, LA = leaf area, SLA = specific leaf area, WD/SD = wood density or stem density, SM = seed mass. Orange lines correspond to average (± CI, light orange) dissimilarity values for the assemblages of three species with low (left, n = 67) or high (right, n = 68) complementarity generated by a random process (see text). Each diagram also shows the assemblages conformed by species with high socioecological suitability and low (TOQ, CBP, and CQP) or high (BrIL, IAK, and CoAK) complementarity used in our study case (see Table 2). These assemblages are indicated by polygons with different dashing. Dissimilarity values range from 0 (full similarity) to 1 (full dissimilarity). Dissimilarity values were calculated using the dissimilarity Marczewski–Steinhaus index (Podani 2000) separately for each trait.

for constructing assemblages. As indicated in the Methods section, we recommend having more than five species per social-ecological category, which reduces redundancy in species composition. In our case, none of the assemblages with the highest FC (top 5% MFAD values) shared the same species composition.

Case Study

In contrast to previous protocols, which primarily targeted ecological restoration (e.g. Ostertag et al. 2015), ours is specifically designed for practical implementation in productive restoration, focusing on AFS (e.g. Schwarz et al. 2021). This approach contributes to the trait-based development of AFS on degraded lands and their potential role in global restoration endeavors (FAO 2017).

This protocol is the result of an iterative field implementation process. A primary challenge during species and assemblage selection was the gradual reduction of viable species, largely due to the end of fruiting seasons. This highlights the importance of efficiently identifying, collecting, and organizing essential information on species and assemblages to maximize the pool of viable options. In this regard, the protocol supports this process by identifying key variables and guiding their management to prioritize and select species and assemblages.

Specifically, we recognize that gathering information on viable tree species will streamline the selection process and expand the potential species pool for restoration. Therefore, it is feasible to identify tree species suitable for ecological restoration as they may share key characteristics with those of interest for AFS. Moreover, these species may have more readily accessible information, and local people may already be familiar with their propagation methods. In this study, the viable tree species largely coincided with those of ecological restoration importance (Meli et al. 2014), and people were familiar with propagating these species through ecological restoration projects in the region.

Also, we recognize that it is paramount to validate the species characteristics obtained from the literature, whether ecological (e.g. rectifying fruiting periods) or social (e.g. confirming the species' utilization in the region). Our study identified discrepancies, even when comparing data collected remotely (e.g. via telephone) with data recorded during field surveys, even for the same locations.

Additionally, appreciation and management of species can vary among communities at local scales. For example, in the MdC region, different local communities utilize various cultivation systems (Wies et al. 2023). To enhance the efficiency of the validation process, it is recommended that a preliminary list of potential species with relevant information and photographs be prepared for field validation with local people. This approach is crucial for determining the actual availability of species based on technical variables, such as the availability of propagules at the site and the local capacity for propagating species on-site or within the region.

Moreover, we observed that collecting information on the importance and local knowledge related to species management can be simplified using a survey with four key questions: for

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each species, "Do you recognize this species?," "Do you use this species?," "Do you cultivate this species?," "Are you interested in cultivating this species?". This approach can facilitate gathering information on the importance and the existing local knowledge related to species management. It is advisable to ask these questions within the context of the specific AFS of interest, determining whether the interest in cultivation lies in self-consumption or extensive cultivation, which influences the species' perceived relevance and suitability for restoration with AFS.

Finally, we consider that integrating a gender perspective into the process is crucial, primarily because gender-related disparities exist in the knowledge and use of vegetation by species and life forms (Suárez 2008). This distinction is particularly important in AFS, as it encompasses diverse interests and ways of life. While, in our study, women were included in various project stages, their involvement was not systematic. Their participation was mainly in workshops, potentially contributing to the high number of recorded useful herbaceous species, accounting for 58% of the cataloged species. Beyond the potential increase in viable species, integrating a gender approach addresses users' distinct contributions and needs, enhancing the restoration efforts' overall success (de Siqueira et al. 2021).

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Supporting Information

The following information may be found in the online version of this article:

Table S1. List of papers from the systematic literature review on functional complementarity in plants or vegetation systems.
Table S2. Description of articles on functional complementarity.
Table S3. List of useful tree species.
Table S4. Discarded tree species during the second filter of the species selection protocol.
Table S5. Viable species of trees resulted from the species selection stage of the protocol.
Table S6. Useful herbaceous and shrub species in the region.
Table S7. Useful herbaceous and shrub species in the region discarded during the species selection process.
Table S8. Viable species of crops and shrubs resulted from the selection stage of the protocol.
Table S9. Assemblages with contrasting levels of complementarity eliminated during the assemblage selection stage.
Supplement S1. Details over a systematic literature review.
Supplement S2. Locality of the case study.

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