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Unleashing the Power of Plant Structural and Functional Diversity: From Common Observations to Theory and Management Models

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ABSTRACT

New approaches for managing agricultural and forestry systems are needed to bring back inputs to levels that are within planetary boundaries and make greater and better use of ecosystem services based on biodiversity. A new scientific framework informed by ecology, agronomy, forestry, and agroforestry is key to designing resilient plant-based ecosystems to meet this challenge. Integrating information on plant functional traits, ontogenetic development stages, site characteristics, and structural stand characteristics can unleash the power of diversity (in species traits and structural and temporal arrangements) as a crucial factor for sustaining environmental services in times of global change. To leverage the benefits of diversity, a general theoretical framework and scalable simulation models are needed to understand structural and species diversification effects and interactions at multiple levels, from plant to field/forest stand to landscape. By working across established research boundaries, the scientific community can harness the power of structural and functional diversity to develop resilient, production-oriented ecosystems. With this integrative approach, our objectives are as follows: (i) to conceptualize processes and methodologies for managing resilient terrestrial ecosystems that can guarantee sustainable and diversified ecosystem services within planetary boundaries, and (ii) to outline the workflow for crafting a system capable of sustaining human well-being amid space, resource, and energy constraints.

1 | Introduction

Over the last 100 years or so, agricultural and forest sciences have developed into separate disciplines, fostered by the overall trend toward scientific specialization (Puettmann, Coates, and Messier 2009). Modern agriculture has been shaped by the Green Revolution, which introduced high-yield crop varieties that rely heavily on large amounts of fertilizers and pesticides (Evenson and Gollin 2003). In forestry, the traditional tendency toward monocultures has intensified, as they seem advantageous for stand establishment, wood production, and forest management (Yaffee 1999; Pretzsch and Zenner 2017). This has led to lower biodiversity and greater separation of forest and agricultural elements in landscapes.

Despite the historical divide between landscape management and scientific research, both fields have independently developed similar concepts and theories. Examples include research on self-thinning in agricultural and forest science by Yoda et al. (1963, 1965) and Reineke (1933), allometric research by Weiner and Thomas (1992) and Enquist et al. (1999), or assessment of facilitation, competition, and overyielding by Vandermeer (1989) in agriculture (Figure 1) and Pretzsch et al. (2010) in silviculture (Figure 2). Scientific achievements related to ecological interactions among species in both areas reflect remarkable convergence of scientific thought that transcends the apparent separation between agricultural and forest sciences, but integration of outcomes is lacking. Experimentation in tree and crop systems has focused mainly on mixtures of two species in the short term, but comparatively little work has been done on multispecies systems or over longer time spans (Pretzsch et al. 2015; Li et al. 2020). Examples of long-term studies are few and include Pretzsch et al. (2019) for forestry, and Garcia-Barrios and Dechnik-Vazquez (2021), Cong et al. (2015) and Li et al. (2021) in crop systems. For instance, a functional trait framework has been proposed to better integrate nitrogen-fixing cover crops into short-rotation woody crop systems, highlighting the need for cross-disciplinary approaches to managing these systems more effectively (Ferreira and Aubrey 2023). We see both a strong need and great potential for common databases and experiments to develop research, knowledge, and prediction models, and for demonstration plots to exhibit new integrative management approaches.

A solid theoretical framework is needed to support the development of a unified approach to managing diversity across terrestrial ecosystems. Joint, cross-domain theories and applications have not yet been developed due to the dominant silo approach in the sciences, combined with the difficulty and low rewards of integrative, synergetic studies. To change this panorama, we advocate the use of plant functional traits (PFTs) to facilitate integrated research and management of forest and agricultural ecosystems. Combining PFT data with species, genotypes, ontogeny, dynamic and interaction patterns, and management types can help move us beyond current challenges to potential solutions. Recent reviews highlight how designing, modeling, and auditing ecosystem service provision in intercropping and agroforestry systems require an integrated approach to address the complexities and trade-offs involved (Rafflegeau et al. 2023), while forests diverse in species, genotypes, ages, and structures, given their greater biodiversity and complementarity of niches, are proposed as suitable for water cycle regulation, carbon storage, and the provision of other ecosystem services (MacKenzie, Ullah, and Foyer 2024). By synthesizing insights from agronomy, forestry, and agroforestry—despite their historical independence—and emphasizing integrative ecological concepts, we can harness the power of diversity to fortify ecosystem health and sustainability that will ensure the provision of ecosystem services and functions.

2 | The Challenge: Integrating Agronomy and Forest Science Research and Management

2.1 | Integration Versus Segregation

The negative effects of the Green Revolution in agriculture (e.g., erosion, pesticides, decreased water quality, and biodiversity) and of far-from-natural monocultures in forestry (e.g., increasing storm damage, insect outbreaks, and soil acidification) are now obvious. This has brought the entire green sector into disrepute and under suspicion jeopardizing sustainability,

FIGURE 1 | Crops in mixtures. Organic strip cropping experiment with cabbage and oats in Wageningen, The Netherlands (left), and intercropping of wheat, soybean, and maize in farmers' practice in Gansu Province, China (right). Photos: Wopke van der Werf.

FIGURE 2 | Forestry is transitioning from rather homogeneous monospecific stands to more diverse mixed stands (left to right). Photos: Chair of Forest Growth and Yield Science, TUM.

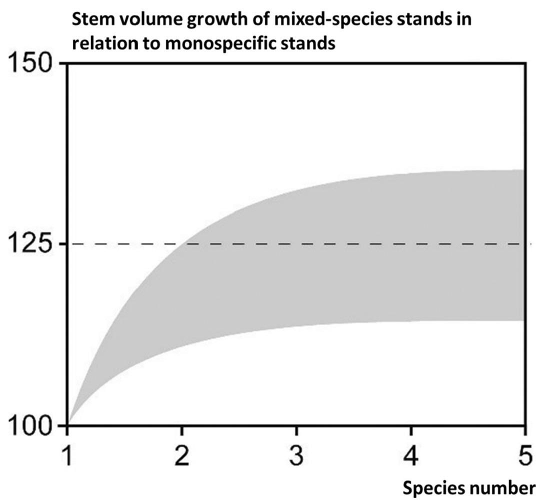

FIGURE 3 | Increased productivity with increasing tree species richness based on worldwide forest inventories, following Liang et al. (2016) and Pretzsch (2019, 329).

although the sustainable management paradigm originated in the forest sector (Carlowitz 1713). Rousseau (1762) argued that nature might do best without human interference, and more recently, Pittelkow et al. (2015) observed that huge portions of the landscape may be entirely protected while others are managed intensively. On the other hand, integrating nature conservation with production provides an alternative to this segregation (Boncina 2011). Anyhow, humans are an important part of the system. In fact, in densely populated areas of Europe such as the Alps, where people use agricultural and forest areas for both livelihood and recreation, the option of segregating and setting aside separate spaces for these two sections is not practicable. However, in areas where ecosystem services such as recreation value, aesthetics, biodiversity, food, and wood production are required of larger spaces, integrating sustainable management and conservation efforts in forestry and agriculture has high potential for reconciling needs and stakeholder interests (Aggestam et al. 2020).

2.2 | Diversification as a Tool for Integrative Management Concepts

Diversification through spatial or temporal combinations of different plant species or farm animals at the stand or landscape level can be a powerful tool for delivering various ecosystem services. Traditional diversification approaches such as agroforestry (Sousa-Silva et al. 2024) or forest selection by harvesting trees to promote a multiaged state or complex structure forests, along with new experiments (Liang et al. 2016), demonstrate this potential. Biological, knowledge-based design can create mixed-species systems overyielding monocultures (Figure 3) and provide other advantages such as higher carbon (C) storage and resilience against (a) biotic stress or biodiversity loss/increase (Wei and Gosselin 2023). Monocultures are certainly easier in terms of establishment, planning, management, and technology. But diversified, mixed systems pave the way to synergy, integrated ecosystem services, and public acceptance.

In recent decades, agriculture and forestry have made great strides in analyzing multicriteria sustainability through diversification. However, these developments have mostly taken place within the separate realms of agriculture and forestry and uptake is limited in practice. For example, TreeDivNet experiments have demonstrated the potential of species mixing to enhance tree performance, yet important research gaps remain, particularly in the long-term integration of these findings into practical forestry applications (Depauw et al. 2024). Like the separation of agricultural and forestry systems that is visible in the landscape, the administration, research, and education aspects of the disciplines have also drifted apart. Agroforestry, for instance, has been shown to significantly contribute to ecosystem services such as biodiversity conservation and erosion control, especially in sensitive environments like karst landscapes (Yang, Xiong, and Xiao 2024). It is time to reverse this institutional divergence and create a common knowledge base for the intelligent resource-efficient design, establishment, and management of sustainable ecosystems that combine agricultural and forestry components at stand or landscape level to favor an enlarged set of ecosystem services (Birthisel et al. 2020).

2.3 | Overcoming Institutional and Scientific Barriers

At present, agriculture and forestry are mainly associated through universities, university departments, and research stations. Bringing trees back into crop systems involves reintegrating trees and tree stands in the agricultural domain, and vice versa. Through closer cooperation, agronomy and forestry will benefit greatly from deeper insights into diversification effects. New integrative educational efforts through joint curricula (such as the dual agronomy and forestry degree at the University of Valladolid) and ecologically sound background and didactic approaches can promote diversity and unleash its power to cope with climate change and ensure ecosystem services provision. For this, the well-established marteloscope method for simulating, educating, and demonstrating the beneficial effects of integrative forest management on ecosystem services (Krumm et al. 2019) could be expanded and adapted to agricultural ecosystems and agroforestry systems.

3 | The Potential of Plant Diversification

In agriculture, there is an urgent need to develop the capacity to carefully craft plant community mixtures for improved productivity, resilience and ecosystem service delivery. Similarly, forestry also seeks sustainable productivity, resilience to disturbances, and provision of ecosystem services through well-designed mixtures (Pretzsch and Zenner 2017). Studies show that mixtures significantly outperform monocultures in yield (Yu et al. 2015; Martin-Guay et al. 2018; Li et al. 2020, 2023), stability (Jucker et al. 2014; Raseduzzaman and Jensen 2017), and resource acquisition (Tang et al. 2021). Managing interactions in mixed crops and agroforestry systems involves combining diverse species traits in a spatial-temporal design that balances positive (e.g., mutualism and facilitation) and negative (e.g., competition and parasitism) interactions (Justes et al. 2021; Hart 2023). The mosaic of traits in plant mixtures—phenology, growth, roots, and physiology—optimizes resource acquisition, stabilizes production, and fosters beneficial organisms (Forrester 2014; Trogisch et al. 2021; Li et al. 2020). The challenge is to create site-specific compositions tailored to local objectives and constraints, with species, ontogenetic stages, and management that will achieve the desired performance outcomes.

Knowledge from agroforestry systems reveals the complex interplay between the benefits and drawbacks of plant mixing (Sousa-Silva et al. 2024). Soil fertility, climate buffering, pest control, and resource competition depend heavily on factors such as resource availability, climate, plant density, and species traits. For example, facilitation of grass growth under trees is more frequent in drier ecosystems, especially when the trees fix nitrogen (Mazía et al. 2016). Battipaglia et al. (2017) highlighted the importance of intercropping with a suitable nitrogen-fixing species to ensure high productivity and water use efficiency of target tree species in Mediterranean agroforestry systems. They also emphasized the need to understand how species interactions change over time and space to establish management criteria that maximize tree performance. However, forest productivity due to climate change losses can be mitigated but not compensated using mixtures in temperate mixed forests (Rodriguez de Prado et al. 2023; Vospernik et al. 2024). In pastures and grasslands, legume–grass mixtures can even outperform monocultures by boosting nitrogen uptake through both symbiotic and nonsymbiotic pathways. Ironically, N fertilization can reduce legume cover, richness, and biomass (Tognetti et al. 2021). Similarly, shade can reduce yield by intensifying competition, but it can also enhance crop quality, as seen in coffee and forage grasses. Tree cover also improves soil fertility, erosion control, and ecosystem diversity (Howlett et al. 2011; Torralba et al. 2016).

The substantial potential of PFTs complementarity for optimizing plant mixtures requires careful consideration of the spatial and temporal contexts influencing individual performance. Functional–structural plant modeling has emerged as a valuable tool for analyzing plant–plant interactions and predicting how structural complexity or spatial arrangements can achieve objectives such as yield optimization (Bravo and Guerra 2002; Evers et al. 2019). However, fully harnessing this potential requires broader understanding of ecosystem services, deeper insights into their underlying mechanisms, and effective management strategies. Numerous studies have examined the impact of plant mixtures on productivity and stability, but key questions remain unanswered. How do plant diversity and system structure affect essential services like climate regulation, biodiversity, and soil fertility? Can we manage mixtures to minimize trade-offs and maximize synergies between ecosystem services? By integrating knowledge about how targeted services are related to plant traits, plant–plant interactions, environmental influences, and other trade-offs, we can move productive agroecosystems beyond traditional monoculture limitations to achieve optimal yield along with a suite of ecosystem services such as improved carbon sequestration, biodiversity, and soil fertility. Integration of field experiments, in situ measurements, and modeling would provide invaluable insights into these mechanisms and unlock the potential of diversified landscapes that thrive ecologically and economically.

4 | Optimization of Plant Functional Traits for Mixture Performance by Matching Species, Genotypes, Patterns, Ontogeny, and Management

PFTs are heritable characteristics that define how a plant functions in relation to photosynthesis, nutrient uptake, reproduction, and so on. They can be categorized into plant size metrics, leaf traits, root traits, and reproductive traits (Cornelissen et al. 2003). PFTs dynamically adapt to growth environments; they influence and are influenced by plant interactions in mixed-species stands (Evers et al. 2019). These traits determine ecosystem functioning, community structure, and spatial and temporal assembly in natural and managed environments through their role in plant functioning, and indirectly by modifying the environment. Matching PFTs in species mixtures to the specific environment and desired performance outcomes requires intricate insight.

Within ecosystems, species adjust their traits based on environmental cues and neighboring plants in a phenomenon known as phenotypic plasticity. This, along with ontogeny (developmental changes from seedling to maturity), affects community assembly, species coexistence, and overall ecosystem performance. The quest continues, however, to discover how functional and structural trait dynamics can be managed to optimize and build sustainable, resilient terrestrial ecosystems that provide essential ecosystem services such as food production, carbon sequestration, and nutrient cycling. In agronomy, this means that the familiar challenge of G×E×M (Genotype × Environment × Management) acquires complexity with the inclusion of genotype interactions (G×G×E×M). In practical terms, which species combination, configuration, and management option will best achieve certain performance objectives in a given local production context? A new crop diversification paradigm is needed to address this question.

Research efforts on mixtures have traditionally been confined to specific domains such as annual crop agronomy (Vandermeer 1989), forestry (Pretzsch et al. 2010) or agroforestry (Sánchez 1995), which hinders comprehensive understanding of plant interactions across the spectrum of plant forms. Bridges among disciplines, especially agriculture, forestry, agroforestry, and ecology are crucial for advancing theoretical knowledge and practical applications.

While interest in diversified crop systems is growing, breeders have only very recently started to explore functional traits conducive to performance in multispecies stands. Breeding for diversified crop systems is still in its infancy compared to breeding for single-species crops, largely because of the increased complexity associated with breeding for mixtures. We are convinced that this hurdle can be overcome with a new general theory of plant mixing, rooted in ecological theory, domain-specific theories, and with data integration from observations, experiments, simulations, and meta-analysis of existing research and traditional knowledge.

An innovative theoretical framework must undergo testing with global empirical data, integrating diverse datasets to estimate ecological relationships across species combinations, management practices, and production environments. Incorporating selected functional traits, ontogeny, site characteristics, and density would enable the development of an integrative theory for the role of functional complementarity in trees, annual crops, and crop–tree mixtures.

To arrive at such integrated approaches, processes must be defined that support resilient terrestrial ecosystem design, to provide sustainable systems and diversified ecosystem services with inputs and outputs that respect planetary boundaries. Success will depend on expertise in many areas, specialized datasets, facilities, and large collaboration networks. Standardized measurements for PFTs, ontogeny development phases, and ecosystem services metrics facilitate mathematical and statistical modeling, upscaling, and the demonstration of operational proof of concept.

5 | Overcoming Obstacles and Finding Solutions

Transitioning from intensively managed arable and forest lands to plant mixtures, intercropping, agroforestry, and mixed forests generates multiple perspectives. Challenges and threats accompany the design and implementation of such options but also opportunities and strengths (Figure 4). For example, Laroche et al. (2019) highlighted how social factors have greater influence than biophysical factors in decisions to adopt intercropping and species mixtures as an operational management alternative. Only recently has a view of ecological succession emerged that integrates human activities as a crucial part of a theoretical framework in which forest succession is considered a socioecological process (Poorter et al. 2024) while the role of humans has, until very recently (at least until 2015), been largely ignored.

Some of these challenges must be addressed before specific guidance about enhancing facilitation in crop and forest systems can be offered to the agricultural and forestry sectors. They include quantifying facilitation, understanding the functional traits that might optimize facilitation, identifying coexistence mechanisms (Spaak and Schreiber 2023), and integrating all these traits into alternative management strategies. The silo approach has hindered our comprehension of the interplay between social factors and biophysical dynamics, thereby slowing the adoption of intercropping and species mixtures for sustainable land management.

The extensive, multifaceted repercussions of prolonged agricultural and forestry practices geared toward industrialized production systems include biodiversity loss, habitat disturbance, reduced complexity, soil compacting by agricultural machinery, nutrient mining, and soil loss in forestry. Landowners or managers adopted these practices to stay competitive. Reversing them can be challenging because it requires a change in the socioeconomic environment (markets and regulations), and often in legal frameworks, to make new approaches attractive to practitioners.

The resistance adoption of the Green Deal in the European farming community in early 2024 (Malingre 2024) clearly demonstrated how innovative production approaches require a facilitating environment that entices practitioners to adopt new practices for long-term benefits and profitability. Alternative production systems exist but often run contrary to prevailing trends that prioritize yield over resilience. Although the

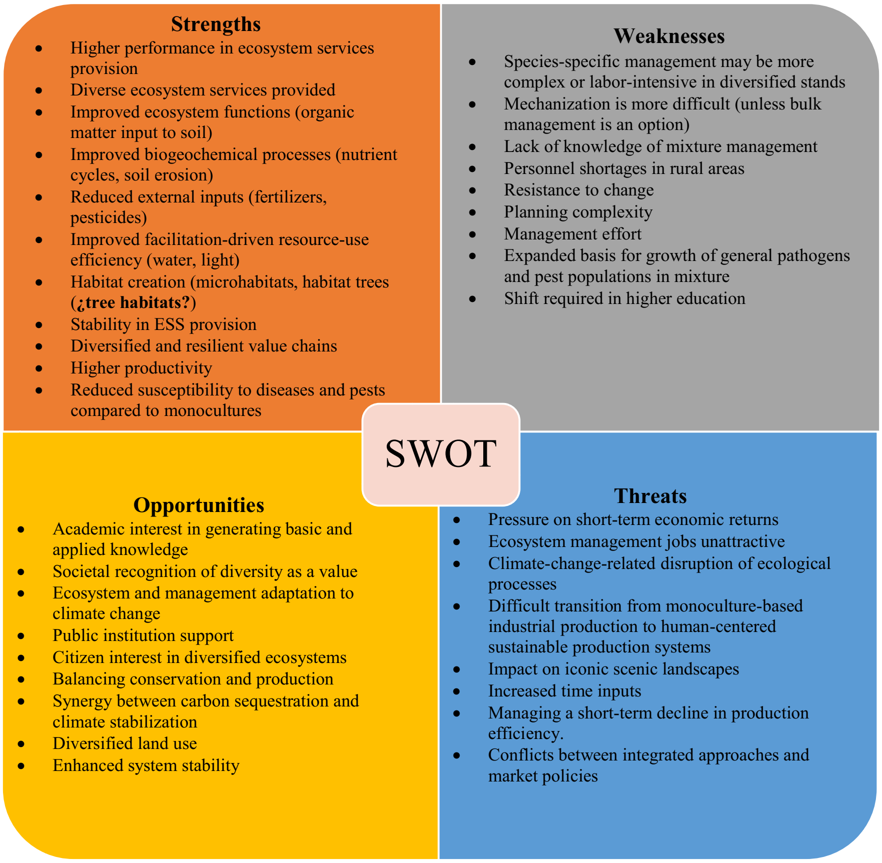

FIGURE 4 | SWOT analysis: The strengths, weaknesses, opportunities, and threats involved in promoting plant-based ecosystem diversity.

numerous advantages resulting from species (and genotype) mixtures extend beyond anthropocentric benefits such as yield stability or carbon sequestration, these positive outcomes are not without associated costs and challenges. Adapting mixtures to local environmental conditions, harmonizing management strategies, aligning with utilization processes, and meeting market requirements pose policy challenges that currently hinder the widespread adoption of alternative approaches (Harvey et al. 2008; Brannan et al. 2023).

A comprehensive theoretical framework and simulation models can help uncover the impacts of structural and species diversification. They also enable scalability, from individual plants to crops, stands, and landscapes. Integrating functional traits, site characteristics, system design, and management goals may yield insights into plant community dynamics, driving factors, and diversity features. The goal is to formulate strategies for managing resilient, globally applicable terrestrial ecosystems that integrate knowledge across disciplines for effective implementation while integrative codesign is crucial for developing useful decision support systems (Bateman et al. 2023) for its development and application. Numerous options exist for managing mixed systems to promote climate mitigation, biodiversity conservation, and system resilience, all of which are scalable. However, inherent trade-offs call for unified metrics that comprehensively integrate empirical research findings into a theoretical framework founded on harmonized data–model integration approaches, common databases, and indicators of social-ecological sustainability across scales and processes. Given the prevailing preference for monoculture in both food and wood sectors, alterations to crop and forest system composition will impact the sector substantially and require adaptive measures. Ultimately, the true challenge lies in the decision to act.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors have nothing to report.

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