

Farmer-reported tree species richness and local knowledge across a land use intensification gradient in upland farming systems of Laos and Vietnam

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ARTICLE INFO

Keywords:

Agroforestry mosaics
β-diversity
Ethnobotanical knowledge
Natural regeneration
Landscape heterogeneity
Tree seed systems
Ecosystem services

ABSTRACT

Smallholder farming landscapes cover large areas of the biodiversity hotspot of the Greater Mekong Subregion and are undergoing rapid land use change driven by economic development, agricultural intensification, and market integration. Yet, their role in maintaining tree diversity, associated ecosystem services, and local knowledge in the ongoing land use transitions remains poorly understood. We assessed perceived on-farm tree species richness, management practices, and species' cultural importance in upland mixed farming systems, across a land use gradient from extensively managed farms in northern Laos to those intensively managed in northern Vietnam, based on interviews with 371 farmers across five provinces and using species richness as metric for α-, β-, and γ-diversity. The results revealed remarkably high α-diversity (425 tree species), particularly in Laos (297 species), where it was mainly associated with natural regeneration. Vietnam's smaller and more intensely managed farms, with mainly planted trees, harbored somewhat lower α-diversity but it was partly compensated by higher β-diversity between farms and landscapes. Tree species' cultural importance and associated knowledge mirrored these patterns, being broadly distributed across multipurpose species in Laos but concentrated around a small number of income-generating species in Vietnam. The proportion of globally threatened species was overall low, but the presence of some threatened taxa in smallholder farming landscapes highlights their potential conservation value. Our findings underscore the importance of supporting natural regeneration, integrating native species into production systems, and strengthening seed and knowledge systems to sustain multifunctional tree diversity in smallholder agricultural mosaics.

1. Introduction

Forests continue to decline and degrade globally, particularly outside protected areas, despite the recognition of the importance of trees among local communities (FAO, 2025). In agricultural mosaic landscapes, some trees are usually retained during forest conversion and serve multiple functions, such as the provision of timber, food, fuel, medicine and regulating ecosystem services, while acting as biodiversity reservoirs and maintaining landscape connectivity (Dawson et al., 2013; Sun et al., 2026). However, such land uses are often transitory and can

gradually lose ecological complexity as land management becomes more intensified and profit-driven (Pfund et al., 2011), which in turn reduces ecological resilience and increases dependency on external inputs in production systems and livelihood vulnerability (Castella et al., 2013; Rasmussen et al., 2018). Land use change can affect biodiversity patterns differently across spatial scales, with within-farm tree diversity, between-farm turnover and landscape-level diversity responding differently to intensification and management practices (Rerkasem et al., 2009; Karp et al., 2012; Sebald et al., 2021). The central challenge, therefore, is how to maintain landscape connectivity and

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<https://doi.org/10.1016/j.tfp.2026.101365>

complexity, and preserve biodiversity and key ecosystem functions during land use transitions, while empowering local communities to meet their economic and socio-cultural development needs (Nguyen et al., 2023; Rahman et al., 2023; Sun et al., 2026).

Achieving a balance between conservation and economic objectives is especially crucial in biodiversity hotspots, such as in Laos and Vietnam in the Greater Mekong subregion. The two countries are home to thousands of endemic and threatened plant species (Park et al., 2018; Nguyen et al., 2023), but have, over recent decades, undergone rapid tree cover changes resulting from population growth, economic development, and agricultural expansion and intensification (Kim and Alounsavath, 2016; Rao et al., 2021). The (still ongoing) transition from subsistence agriculture to commodity cropping is driven by market demand, technological changes, and government policies (Meyfroidt and Lambin, 2008; Jadin et al., 2013). The expanding areas of settled agriculture and tree plantations have favoured monocultures such as rubber, coffee, bamboo, maize, and others (Meyfroidt et al., 2013), with the resulting economic gains coming at the expenses of forests, biodiversity, and ecosystem services (Appelt et al., 2022). This trade-off is an increasingly pressing issue in the subregion, as countries seek to reconcile poverty reduction with environmental sustainability goals. Various policies and initiatives to address deforestation since the 1990s have yielded mixed results, with tree cover recovering in some areas and further declining elsewhere (Kim and Alounsavath, 2015; Phompila et al., 2017; Cochard et al., 2020; Nguyen et al., 2024).

In northern Vietnam and northern Laos, high biodiversity overlaps with numerous ethnolinguistic groups including H'Mông, Tày, Thái, Dao and Khmu, resulting in exceptional biocultural diversity. Traditionally, these groups managed mosaics of crop fields, rotating swidden plots, and homegardens, and collected forest products for subsistence or small-scale trade, guided by traditional ecological knowledge (TEK) of tree species, their uses, traits, and management practices (Yokoyama, 2004; Nguyen et al., 2024). While the groups have adapted to the changing world in different ways, from embracing market integration to expanding traditional practices (Ohlsson, 2009; Turner and Pham, 2015; Whitney et al., 2016; Chen et al., 2023), traditional knowledge continues to play a role in shaping decisions on land use and biodiversity management in agricultural landscapes (Boissière et al., 2009; Choocharoen et al., 2014; Whitney et al., 2016).

Amid these broad changes, tree diversity, associated traditional knowledge, and their role in supporting livelihoods in the northern Greater Mekong subregion remain understudied. Ethnobotanical research has uncovered traditional knowledge on medicinal plants and wild food species among different ethnic groups (Whitney et al., 2014; Dubost et al., 2019; Nguyen et al., 2019), while participatory research has connected such knowledge systems to ecosystem services, conservation priorities, and community-based forest management (Boissière et al., 2009; Nguyen et al., 2020). These studies have primarily focused on forest-dependent communities or protected area contexts, and rarely examined farmer-managed landscapes. In particular, how species richness and associated traditional knowledge vary across the transition from extensively to intensively managed systems, and what it means for conservation and livelihood outcomes, remains unknown for northern Laos and Vietnam, a gap that our study addresses.

The objective of this study was to assess perceived tree diversity, associated local knowledge, and their contributions to local livelihoods and conservation goals in farmer-managed landscapes of northern Laos and northern Vietnam. The study sites in the global biodiversity hotspot represent a gradient from low human population density and generally extensive land uses in northern Laos (including a large proportion of naturally regenerating pastures and fallows) to high human population density and more intensive land uses with deliberate tree planting (i.e. commercial agriculture and tree plantations) in northern Vietnam. The specific research questions were: (1) How does tree species richness vary by farm size and across the land use gradient? (2) How do species uses and cultural importance vary across the land use gradient and by tree

origin (natural vs. planted)? (3) To what extent do the surveyed landscapes contribute to the conservation of threatened tree species? (4) Which tree species do farmers perceive as resistant to local stress conditions and most contributing to selected ecosystem services? (5) What motivates farmers to grow or retain trees on farm, and what constraints do they face? We discuss the implications of these patterns for the conservation and management of tree diversity and associated local knowledge in agricultural mosaics undergoing land use transformation.

2. Materials and methods

2.1. Study region

The study was carried out in five provinces in the uplands of northern Laos and Vietnam: Luang Prabang and Xiengkhouang in Laos, and Bắc Kạn, Lào Cai, and Sơn La in Vietnam (Fig. 1). These provinces are characterized by largely rural populations, inhabited by diverse ethnic groups including H'Mông, Khmu, and Lao Loum (ethnic majority) in Laos, and Tày, H'Mông, Mường, Khơ Mú, Thái and Dao in Vietnam. The region belongs to the biome of tropical and subtropical moist broadleaf forests (Dinerstein et al., 2017) and is predominantly composed of mid-elevation uplands ranging from 700 to 1200 m above sea level. The landscapes feature substantial remaining forest cover interspersed with diverse forest-agriculture mosaics (Table 1). Low to moderate tree cover on croplands, associated with scattered trees, agroforestry, or regrowth of fallows (Zomer et al., 2014), is relatively common in Laos, while land uses tend to be more segregated in Vietnam (Table 1). The Vietnamese provinces have a much higher human population density of about 68–125 people km⁻² (National Statistical Office, 2024) compared to just 19–29 people km⁻² in Laos (Lao Statistics Bureau, 2025).

2.2. Land use context

Land use trajectories differ between the two countries. Vietnam is one of the few countries to have recorded a transition from net deforestation to a net increase in forest cover (Meyfroidt et al., 2013; Zimmer et al., 2022). Extensive deforestation occurred between the 1960s to 1990s, driven by a growing human population as well as state-encouraged migration from lowland areas to the highlands (Meyfroidt and Lambin, 2008). With policy changes in the 1990s, deforestation was halted, and tree cover increased from 25% in the 1980s to 42% in 2018 (Meyfroidt and Lambin, 2008; Zimmer et al., 2022). This increase is generally attributed to the prohibition of swidden cultivation, land privatization (which promoted the separation of agriculture and forestry), agricultural intensification, and state-led efforts in forest protection and restoration (Meyfroidt and Lambin, 2008; Cochard et al., 2020). The recent tree cover gains, however, consist mostly of exotic tree plantations, mainly *Acacia* spp. (Zimmer et al., 2022) and, in some areas, natural regeneration (Cochard et al., 2017). Tree cover has also increased on agricultural lands, with coffee (*Coffea* spp.), tea (*Camellia sinensis*) and native and exotic fruit trees such as longan (*Dimocarpus longan*), plum (*Prunus salicina*), and mango (*Mangifera indica*). Despite successes in reversing deforestation, localized forest cover loss and the gradual degradation of remaining forests remain a concern (Cochard et al., 2020).

Land use in Laos has also undergone significant changes over the past few decades, driven by both market and state forces, but agricultural transition and land use segregation between agriculture and forests has been more gradual in comparison to Vietnam (Appelt et al., 2022). In the 1990s, much like Vietnam, Laos implemented policy and legislation changes, aimed at forest conservation in concurrence with international policy developments (Lestrelin et al., 2012), while also prioritizing poverty eradication and relocation of upland communities to lowland areas closer to road infrastructure (Ducourtieux et al., 2005). At the time, the country also began to open itself up to the global market (Ohlsson, 2009). Forest protection and land privatization were

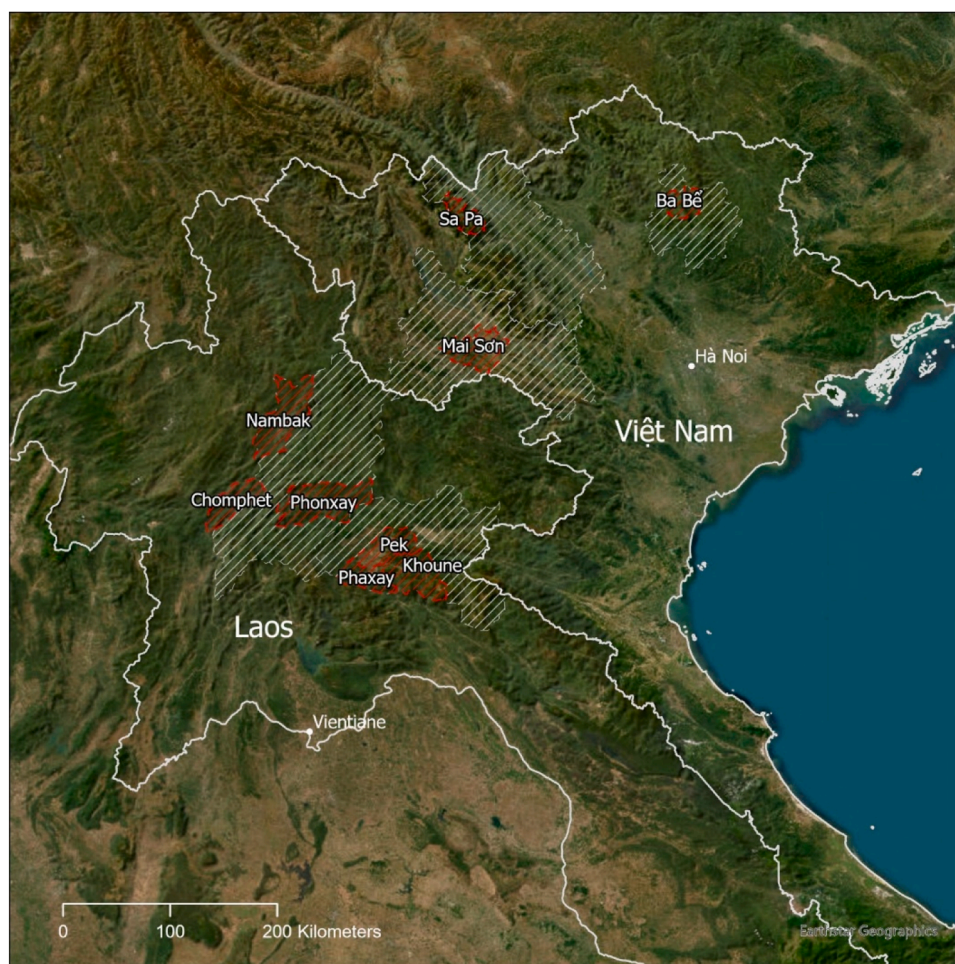


Fig. 1. Geographic location of the study areas in Laos and Vietnam. Lightly hatched white polygons indicate the study provinces, and red hatched polygons indicate the study districts within those provinces. Map lines delineate study areas and do not necessarily represent officially accepted national boundaries.

Table 1

Characteristics of the study districts. Tree cover percentage on croplands and planted trees was derived by overlaying cropland and planted forest areas in the Global Land Cover and Land Use Change dataset (Potapov et al., 2022) and the Spatial Database of Planted Trees (Richter et al., 2024) with the data on tree cover by Brandt et al. (2023).

Country and province	District	Human population density (km ⁻²)	Tree cover on cropland and planted trees		Forest cover, %	No. surveyed villages
			>10% - 40% tree cover ^a	>40% tree cover ^b		
Laos						
Luang Prabang	Chompet	29	20	39	67	6
	Nambak		16	37	69	9
	Phonxay		17	29	70	8
Xiengkhouang	Khoun	19	17	25	72	6
	Phaxay		18	20	74	7
	Pek		20	16	55	7
Vietnam						
Bắc Kạn	Ba Bể	71	11	21	73	15
Lào Cai	Sa Pa town	120	12	34	72	15
Sơn La	Mai Sơn	119	20	22	46	15

^a Open canopy; trees are present but not dominant; e.g. scattered trees on farms, agroforestry, regrowth on fallows.

^b Closed or semi-closed canopy, associated e.g. with tree plantations, coffee plantations, orchards.

promoted alongside intensive farming, as the country transitioned from subsistence agriculture towards a market-based system. Intensive agriculture and forest plantations, including smallholder teak (*Tectona grandis*) and rubber (*Hevea brasiliensis*) plantations, have expanded in upland farming systems along with road infrastructure (Thongmanivong et al., 2009; Newby et al., 2014). Cultivation of tree crops such as coffee and macadamia (*Macadamia integrifolia*) is common in some districts,

although not as widespread as in Vietnam. Despite having a much smaller human population than Vietnam, Laos also faces challenges regarding its forest cover, with particularly the evergreen forests steadily declining (Boundeth et al., 2012; Zhang et al., 2022). Additionally, northern Laos has experienced significant pasture expansion since 2010 (Himel et al., 2024), mainly driven by emerging livestock demand from China and Vietnam.

2.3. Data collection

We documented perceived on-farm tree species richness through household surveys, followed by farm walkabouts to confirm reported species identity where possible. Perception-based approaches are well established in ethnobotanical research (Martin, 2010; Tardío and Pardo-de-Santayana, 2008) and have been shown to provide reliable estimates of tree species richness in agroforestry contexts (Raneri et al., 2021).

Study districts were selected to represent ethnic diversity and variation in land use intensity (Table 1). Three districts were surveyed in each province in Laos and one district per province in Vietnam, reflecting differences in human population density. The surveys employed purposive sampling, targeting villages and households with a history of integrating trees into agricultural production systems. This approach was chosen to maximize the capture of local knowledge on tree species traits, uses, and management practices, which was a central objective of the study, and consistent with ethnobotanical survey designs (Martin, 2010; Tardío and Pardo-de-Santayana, 2008). As such, the sample was not intended to be statistically representative of all farming households in the region, but rather to characterize the range of perceived tree species richness and local knowledge across a gradient of land use systems. Each household was interviewed individually. Enumerators were instructed to interview both men and women in each village, where possible, and in some cases, male and female members of a household were interviewed together.

In Laos, the surveyed villages and households were selected in consultation with the technical staff of the district agriculture and environment offices (DAEO), and in total 120 households (17% female respondents) were interviewed across 43 villages. In Luang Prabang, the majority of respondents identified as Lao (62%), followed by H'Mông (38%). Xiengkhouang exhibited a more diverse ethnic distribution, with H'Mông households making up 50%, Lao 34%, and Khmu 16% of the surveyed population. Overall, across both provinces, H'Mông households accounted for the largest share (44%), followed by Lao (48%) and Khmu (8%).

In Vietnam, the surveyed communes were selected in collaboration with the Departments of Agriculture in Mai Sơn district in Sơn La province, and Ba Bê district in Bắc Kạn province, as well as the Economic Department in Sapa town, Lào Cai province. The survey was carried out in three villages per commune and with 5–6 farming households per village, for a total of 251 households (29% female respondents) across 45 villages. In Bắc Kạn, the dominant ethnic groups were Tày (47%) and Dao (35%), followed by H'Mông (7%), Kinh (7%), and Nùng (4%). Respondents in Lào Cai were primarily H'Mông (60%), with smaller populations of Dao (16%), Tày (15%), and Dáy (10%). Sơn La stood out for its ethnic homogeneity, with 100% of surveyed participants identifying as Thái. Overall, the sample consisted of Thái (33%), H'Mông (22%), Tày (21%), Dao (17%), Ngáy (3%), Kinh (2%), and Nung (2%).

Structured survey questionnaires included closed-ended questions on household characteristics, land ownership, and land uses, and open-ended questions on reasons for integrating trees in the farming system, important tree species for the household and their uses and traits, species that had disappeared from the landscape, preferred species for planting, constraints to growing trees on farm and areas of support needed. The surveys were conducted primarily in the national language (Lao and Vietnamese, respectively), but with occasional translation to the local minority languages. To validate farmer-reported species identifications, walkabouts on the farms were carried out where possible to confirm species identity and collect botanical specimens or photos of species which could not be easily identified. Walkabouts were not based on a formal transect protocol but were instead guided by farmers based on the list of species they had reported, and the distance covered depended on the farm layout and accessibility. Local names were cross-referenced with botanical references and checklists (e.g. Hoang et al., 2004; Wei et al., 2022) and verified by local experts where scientific

identification was uncertain. However, field validation was not always possible, especially in Vietnam where farmlands were often far from the homesteads. In total 54 species, mostly mentioned by individual respondents, could not be identified, mainly among the Thái ethnic group in Vietnam's Sơn La province, due to the inaccessibility of distant fields for validation and the difficulty of matching local species names in ethnic minority languages with scientific names (Table S7).

Ethical clearance for the research was provided by the Institutional Review Board of Bioversity International (ID: 2022-IRB39 for Laos and 2023-IRB49 for Vietnam), and all research activities were performed in compliance with relevant laws and institutional guidelines in the countries of research. Free and Prior Informed Consent was obtained from all research participants, and their privacy rights were observed.

2.4. Data analysis

2.4.1. Ethnospecies and perceived species richness

We collected data on trees and shrubs while also including bamboos and palms, all of which will be referred to as 'tree species' for simplicity. The primary unit of analysis was ethnospecies, defined as species identities as locally perceived by indigenous or local communities (Martin, 2010). Ethnospecies are used in ethnobotany to document local ecological knowledge, and as components of ethnotaxonomy, they do not always correspond precisely to botanical taxonomy (Martin, 2010). Ethnospecies can involve under-differentiation, where multiple scientifically distinct species, usually of the same genus, are grouped under one local name due to their high similarity in terms of appearance, uses, or both. In other cases, although rarer, they can also involve over-differentiation, where distinct local names are assigned to what is considered a single species by botanists, sometimes coinciding with different subspecies or cultivars. Using ethnospecies as the unit of analysis allowed capturing all species cited by survey respondents, who often provided only local names. In some instances, identification was limited to the genus level. The 54 ethnospecies which could not be identified in Vietnam were excluded from the analysis, representing 22% of the 242 records from the country, mainly concentrated in Sơn La province.

As the study was interview-based, it was not possible to calculate species diversity indices requiring species abundance data (e.g. Shannon or Simpson). Because our aim was to compare species pools across farms, provinces and countries, we assessed α -, β -, and γ -diversity using (ethno)species richness as metric, following Whittaker's (1972) classical definitions widely applied in floristic surveys. To assess compositional turnover (β -diversity) between countries, we also calculated Sørensen-Dice dissimilarity index based on presence data (Anderson et al., 2006). Throughout this study, 'tree diversity' is used to refer to patterns and variation in tree species richness and composition across farms and landscapes (e.g. Pfund et al., 2011; Dawson et al., 2013), while species richness and α -, β -, and γ -diversity refer specifically to the metrics and analytical levels used in the study.

Differences in species richness per farm, farm size, and number of land uses between the countries were assessed using a Wilcoxon rank-sum test, as the variables were not normally distributed. Differences in the proportions of planted species and threatened species between the countries were assessed using chi-square tests of independence. Species listed as Not Evaluated or Data Deficient on the IUCN Red List of Threatened Species (IUCN, 2025) were excluded from the analysis because the proportion of assessed species varied between the countries.

2.4.2. Culturally important species

To identify the tree species most important for local communities, we calculated the cultural importance (CI) index of the reported species, defined as the sum of the relative frequencies of citation (i.e. the proportion of respondents citing a species) for the different use categories (Tardío and Pardo-de-Santayana, 2008):

$$CI = \sum_{u=U_1}^{U_{NC}} \sum_{i=I_1}^{I_N} \frac{UR_{ui}}{N} \quad (1)$$

where UR_{ui} refers to the use report of use category u by respondent i , N to the number of respondents, and NC to the number of use categories. When only considering one use category, the CI is equal to the relative frequency of citation in that use category. The CI index is equivalent to the simplified version of the use value (UV) index, proposed by Phillips & Gentry (1993) and Tardío and Pardo-de-Santayana, (2008)).

2.4.3. Species' perceived contributions to ecosystem services and resistance to local stress conditions

Respondents were asked to free-list the species they perceived to be the most and the least suitable to deliver selected ecosystem services [erosion control, soil fertility improvement, shade for crops, shade for livestock, fodder (palatability for livestock), and attraction of birds and/or bees] and the species perceived as most and least resistant to different stress conditions (drought resistance, fire resistance, flood resistance). The free-lists were analysed by calculating the composite salience (CS) index, which takes into account both the rank and the frequency of the species in the free-lists (Smith, 1993; Quinlan, 2005):

$$CS = \sum_{i=I_1}^{I_N} \frac{R_i^{-1}}{L_i} \frac{1}{N} \quad (2)$$

The CS index is calculated by first dividing the inverse rank of each species in the list by the total number of species in the list, resulting in the 'salience' of each species in each free-list. Next, the 'composite salience' of each species is obtained by dividing the sum of its salience scores by the number of respondents. The CS index was calculated for both the free-lists of the species perceived as most and least suitable, resulting in two CS values per species, and a ranking of both the most suitable and least suitable species.

3. Results

3.1. Perceived species richness

A very high perceived species richness was reported in both Laos and Vietnam (Table 2). In Laos, where the surveyed households managed land use mosaics dominated by pasture (49%) and fallow land (23%),

297 ethnospecies of trees and shrubs were reported, belonging to 67 families (see Supplementary information, Table S1, for a full list). Sixty-nine ethnospecies (approximately 23%) were mentioned by only one farmer. In Vietnam, where household land use was dominated by forest (43%) and plantation forestry (26%), 188 identified ethnospecies of 59 families were reported (Table S2). Forty-nine ethnospecies (26%) were mentioned by only one farmer. From here onwards, we will refer to ethnospecies as 'species' for simplicity.

Only 60 out of the total 425 identified species were reported in both countries, giving Whittaker's β -diversity of 1.75, and Sørensen-Dice index of 0.75. Half of the overlapping species were fruit trees, including sugar apple (*Annona squamosa*), jackfruit (*Artocarpus heterophyllus*), and mango (*Mangifera indica*), followed by commercial timber species such as *Dalbergia tonkinensis*, *Chukrasia tabularis*, and *Tectona grandis*.

In Laos, farms were larger on average ($W = 20,410$, $p < 0.001$) and supported higher species richness than in Vietnam ($W = 23,239$, $p < 0.001$), but number of land use types per farm was greater in Vietnam ($W = 4420.5$, $p < 0.001$) (Table 2). Smallest farms had the highest species richness per hectare (Table 3, Figure S1), but the Spearman correlation test between farm size and species richness per hectare was statistically significant only in Vietnam ($\rho(250) = -0.3$, $p < 0.05$) and not in Laos ($\rho(120) = 0.1$, $p > 0.05$). Pairwise comparisons with Tukey's HSD showed that average species richness per hectare was significantly higher in Laos than in Vietnam among small and small-medium farms ($p < 0.001$ and $p < 0.0052$, respectively), but not in larger farms of 5 ha or more.

Trees on farms were reported mostly naturally regenerating in Laos (69%) and mostly planted in Vietnam (79%) (Table 2). In Laos, sourcing of planting material was dominated by household efforts, with 56% of households collecting seeds themselves, and 20% buying seeds from traders or markets. Local seed exchange was limited, with only 10% obtaining seeds from people in the same village and 5% from people in other villages. Institutional contributions were similarly modest: 7% from public extension services and other government agencies, and 2% from non-governmental organisations (NGOs). In contrast, in Vietnam, self-collection (31%) and markets (31%) were equally important sources of seed. The role of local exchange (11% from the same village and 3% from other villages), and institutional inputs (6% from public sector and 0% from NGOs) was limited, similarly to Laos.

Table 2

Perceived species richness, farm characteristics and tree origin country and province. CI represents 95% confidence interval (LL represents lower limits; UL represents upper limits). Confidence intervals for size classes with $n \leq 2$ should be interpreted with caution.

Country Province	Richness		Farm characteristics			Tree origin	
	Total number of families	Total number of species (γ -diversity)	Sørensen-Dice index; CI 95% (LL, UL) (β -diversity)	Average species richness per farm; CI 95% (LL, UL) (α -diversity)	Average farm size (ha); CI 95% (LL, UL)	Average number of land use types; CI 95% (LL, UL)	Average percentage of planted trees
Laos	67	297	0.85 (0.85, 0.85)	21.4 (19.2, 23.7)	9.6 (5.8, 13.4)	3.0 (2.8, 3.2)	31%
Luang Prabang	51	186	0.81 (0.80, 0.82)	17.1 (13.8, 20.5)	11.0 (3.4, 18.6)	2.9 (2.6, 3.2)	41%
Xiengkhouang	65	233	0.77 (0.76, 0.77)	25.5 (22.6, 28.3)	8.3 (6.2, 10.4)	3.1 (2.7, 3.5)	25%
Vietnam	59	188	0.76 (0.76, 0.77)	10.9 (10.4, 11.3)	3.6 (3.0, 4.2)	4.9 (4.8, 5.0)	79%
Bắc Kạn	45	97	0.69 (0.68, 0.69)	10.5 (9.7, 11.2)	3.5 (2.9, 4.1)	4.2 (4.0, 4.4)	90%
Lào Cai	45	98	0.72 (0.71, 0.72)	8.6 (8.0, 9.2)	1.6 (1.3, 1.9)	4.5 (4.3, 4.7)	95%
Son La	39	96	0.58 (0.57, 0.58)	13.4 (12.7, 14.2)	5.7 (4.1, 7.3)	5.9 (5.7, 6.1)	63%
Laos x Vietnam^a	NA	NA	NA	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)	($p < 0.001$)

^a Pairwise comparison of each variable between the two countries. Test values are reported in the text.

Table 3

Perceived tree species richness by farm size. CI represents 95% confidence interval (LL represents lower limits; UL represents upper limits). Confidence intervals for size classes with $n \leq 2$ should be interpreted with caution.

Country	Farm type	Farm size (ha)	Frequency	Average number of land use; CI 95% (LL, UL)	Average species richness per farm; CI 95% (LL, UL)	Average species richness per ha; CI 95% (LL, UL)
Laos	Small	< 2	18 (15%)	2.3 (1.7, 2.9)	15.7 (12.6, 18.8)	21.5 (9.9, 33.1)
	small-medium	2 to 4.99	42 (35%)	2.5 (2.2, 2.8)	21.1 (16.6, 25.6)	7.3 (5.8, 8.8)
	Medium	5 to 9.99	28 (23%)	3.0 (2.7, 3.4)	20.9 (16.0, 25.8)	3.1 (2.4, 3.8)
	medium-large	10 to 49.99	30 (25%)	4.1 (3.6, 4.6)	25.3 (20.8, 29.8)	1.7 (1.3, 2.1)
	Large	≥ 50	2 (2%)	3.0 (-9.7, 15.7)	29.0 (-110.8, 168.8)	0.2 (0.0, 0.4)
Vietnam	Small	< 2	95 (38%)	4.1 (3.9, 4.3)	9.3 (8.7, 9.9)	11.5 (9.9, 13.1)
	small-medium	2 to 4.99	99 (40%)	5.2 (5.0, 5.4)	11.6 (10.9, 12.4)	3.8 (3.5, 4.1)
	medium	5 to 9.99	47 (19%)	5.6 (5.3, 5.9)	12.2 (11.1, 13.2)	1.9 (1.7, 2.1)
	medium-large	10 to 49.99	8 (3%)	5.1 (4.4, 5.8)	11.6 (9.1, 14.2)	1.0 (0.7, 1.3)
	Large	≥ 50	1 (<1%)	4.0 (NA)	19.0 (NA)	0.3 (NA)

3.2. Presence of threatened tree species

The proportion of threatened species was significantly higher in Vietnam than in Laos ($\chi^2 = 5.57$, $p = 0.018$) (Table 4). In Laos, most of the reported species were classified as Least Concern (74%), with only 5% (16 species) falling under threatened categories (Critically Endangered, Endangered, or Vulnerable) (Table 4). When asked about which species have disappeared from the local landscape, the respondents (49 farmers) mentioned 10 species, including *Pterocarpus macrocarpus* (Endangered) (20 mentions), *Pometia pinnata* (Least Concern) (10), and *Azela xylocarpa* (Endangered) (5) (Table S3). In Vietnam, 57% of the reported species were Least Concern, while 10% (18 species) fell into threatened categories (Table 4). The respondents (251 farmers) mentioned 49 identified species as having disappeared, including *Syzygium aromaticum* (Data Deficient/Not Evaluated) (31 mentions), *Burretiodendron tonkinense* (Near Threatened) (25), and *Chukrasia tabularis* (Least Concern) (22) (Table S4).

3.3. Species uses

The most reported species uses in Laos were fuelwood (225 species, 76% of all species), timber (154 species, 52%), and food (and drinks) (138 species, 47%). In total 35 species (12%) were reported as forage, 34 species (11%) as medicine, and 47 species (16%) for other purposes, including cultural, ornamental, or ecological. In Vietnam, timber (152

species, 63%) and medicinal uses (47 species, 20%) were more frequent than in Laos, whereas food (99 species, 41%) and fuelwood (72 species, 30%) were somewhat less frequent than in Laos. Other uses comprised 42 species (17%). The cultural importance scores broadly reflected the main species uses: in Laos, focus was on multifunctional trees that provide fuelwood, timber, and food for both household needs and sale, while in Vietnam, focus was on species that provide income (Fig. 2). The scores varied less in Laos than in Vietnam, where cultural importance was concentrated on a relatively limited number of species considered important by many farmers. In Laos, the culturally most important species were mainly naturally regenerating, whereas in Vietnam, they were almost all mainly cultivated (Fig. 2).

3.4. Preferred species for tree planting

Respondents in Laos identified in total 55 tree species that they were interested to plant. These mostly overlapped with species of the highest cultural importance (Fig. 2) and included 28 fruit tree species, 17 timber species, and 10 other economically useful plants (Table S5). Several wild species such as those belonging to *Castanopsis* spp., were not mentioned as preferred for planting despite their high cultural importance, whereas *Dimocarpus longan* was preferred although not identified as holding high cultural importance. In Vietnam, a total of 47 species were preferred for planting, most commonly the timber species *Magnolia conifera* (33 mentions), followed by mostly fruit and nut tree species (Table S6). Out of these, only *Macadamia integrifolia* was not among the 20 culturally most important species (Fig. 2).

3.5. Species' perceived contributions to selected ecosystem services and resistance to local stress conditions

When respondents were asked to free-list tree species they considered the most and least suitable to deliver specific ecosystem services or resist to local stress conditions, several species stood out with consistently positive scores across multiple ecosystem services and stresses, for example, *Pterocarpus macrocarpus* and *Castanopsis hystrix* in Laos, and *Dimocarpus longan* in Vietnam (Table 5). On the other hand, some species were frequently considered unsuitable for multiple purposes: for instance, in Vietnam, *Mangifera indica* was perceived as prone to drought and fire, and unsuitable for erosion control; while *Prunus persica* and *Prunus salicina* received negative scores for flood resistance, erosion

Table 4

IUCN conservation status of the reported tree species on-farm in Laos and Vietnam.

Status	Laos		Vietnam	
	Count	%	Count	%
Critically endangered	3	1	2	1
Endangered	7	2	9	5
Vulnerable	6	2	7	4
Total threatened	16	5	18	10
Near Threatened	4	1	2	1
Least Concern	220	74	107	57
Total assessed	240	81	127	68
Data deficient	8	3	6	3
Not evaluated	49	16	55	29
Total not assessed	57	19	61	32
Grand Total	297	100	188	100

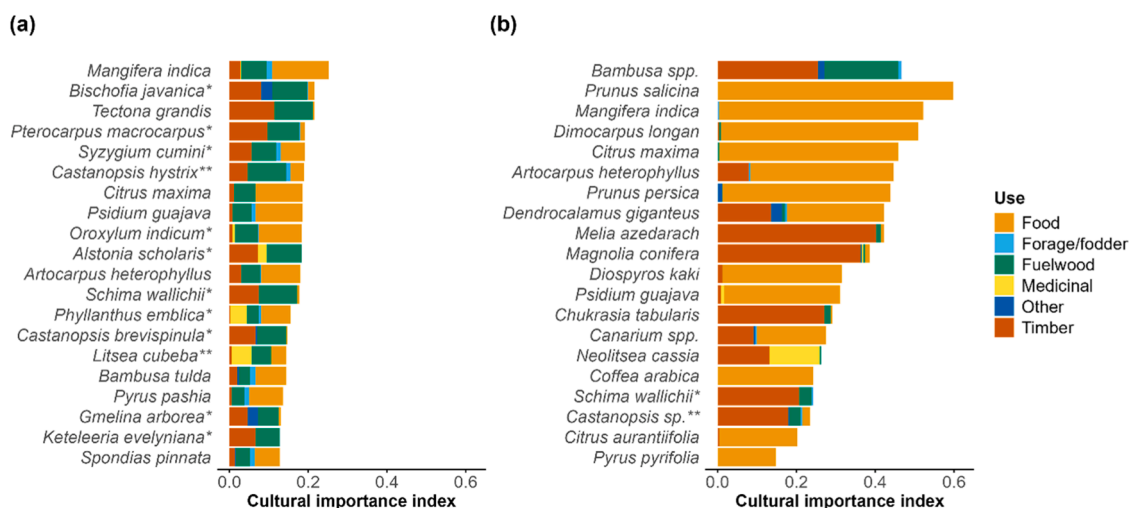


Fig. 2. Species with the highest cultural importance index for (a) Laos and (b) Vietnam.

*mainly naturally regenerating (>50%), **only naturally regenerating, no planting reported.

Table 5

Most and least suitable species in terms of delivery of selected ecosystem services and resistance to local stress conditions, as expressed by composite salience scores derived from the free-lists provided by farmers. Only species with salience scores ≥ 0.03 are shown. Scores reflect farmer-reported perceptions of species suitability, and are not intended as agronomic or ecological assessment of species performance.

	Laos		Vietnam	
	Most suitable species	Least suitable species	Most suitable species	Least suitable species
Ecosystem services				
Erosion control	<i>Bambusa tulda</i> (0.13) <i>Bambusa tuldoidea</i> (0.09) <i>Dendrocalamus strictus</i> (0.08)	<i>Pinus latteri</i> (0.03) <i>Tectona grandis</i> (0.03)	<i>Bambusa spp.</i> (0.23) <i>Dendrocalamus giganteus</i> (0.16) <i>Magnolia conifera</i> (0.08)	<i>Magnolia conifera</i> (0.05) <i>Prunus persica</i> (0.05) <i>Prunus salicina</i> (0.04)
Soil fertility improvement	<i>Bischofia javanica</i> (0.09) <i>Bambusa tulda</i> (0.03)	<i>Tectona grandis</i> (0.07) <i>Castanopsis hystrix</i> (0.05) <i>Pinus latteri</i> (0.05)	<i>Coffea arabica</i> (0.10) <i>Magnolia conifera</i> (0.08) <i>Melia azedarach</i> (0.06)	<i>Bambusa spp.</i> (0.20) <i>Dendrocalamus giganteus</i> (0.13) <i>Magnolia conifera</i> (0.03)
Shade for crops			<i>Dimocarpus longan</i> (0.14) <i>Melia azedarach</i> (0.06) <i>Mangifera indica</i> (0.04)	<i>Prunus salicina</i> (0.07) <i>Dendrocalamus giganteus</i> (0.06) <i>Bambusa spp.</i> (0.06)
Shade for livestock	<i>Castanopsis hystrix</i> (0.13) <i>Bambusa tulda</i> (0.05) <i>Tectona grandis</i> (0.04)	<i>Tectona grandis</i> (0.04) <i>Pinus latteri</i> (0.04) <i>Cratogeomys formosus</i> (0.03)	<i>Dimocarpus longan</i> (0.19) <i>Artocarpus heterophyllus</i> (0.06) <i>Chukrasia tabularis</i> (0.05)	<i>Prunus salicina</i> (0.14) <i>Melia azedarach</i> (0.13) <i>Prunus persica</i> (0.08)
Fodder (palatability for livestock)	<i>Gymnanthemum extensum</i> (0.03)		<i>Broussonetia papyrifera</i> (0.03)	
Attracting birds or bees	<i>Microcos tomentosa</i> (0.04) <i>Pyrus pashia</i> (0.03) <i>Muntingia calabura</i> (0.03)		<i>Dimocarpus longan</i> (0.11) <i>Prunus persica</i> (0.06) <i>Prunus salicina</i> (0.05)	
Resistance to local stress conditions				
Drought resistance	<i>Tectona grandis</i> (0.07) <i>Castanopsis hystrix</i> (0.06) <i>Bambusa tulda</i> (0.04)	<i>Litsea cubeba</i> (0.04) <i>Tectona grandis</i> (0.03) <i>Castanopsis hystrix</i> (0.03)	<i>Dendrocalamus giganteus</i> (0.12) <i>Bambusa spp.</i> (0.08) <i>Dimocarpus longan</i> (0.04)	<i>Magnolia conifera</i> (0.17) <i>Mangifera indica</i> (0.08) <i>Coffea arabica</i> (0.07)
Fire resistance	<i>Tectona grandis</i> (0.12) <i>Castanopsis hystrix</i> (0.09) <i>Pterocarpus macrocarpus</i> (0.05)	<i>Litsea cubeba</i> (0.03) <i>Triadica cochinchinensis</i> (0.03) <i>Senna siamea</i> (0.03)	<i>Bambusa spp.</i> (0.19) <i>Dendrocalamus giganteus</i> (0.13) <i>Schima wallichii</i> (0.05)	<i>Cinnamomum cassia</i> (0.09) <i>Mangifera indica</i> (0.05) <i>Cunninghamia lanceolata</i> (0.05)
Flood resistance			<i>Bambusa spp.</i> (0.16) <i>Dendrocalamus giganteus</i> (0.12)	<i>Prunus persica</i> (0.07) <i>Citrus maxima</i> (0.05) <i>Prunus salicina</i> (0.03)

control, and shade provision for livestock, although they were appreciated for attracting birds and bees. Composite salience scores were generally higher in Vietnam than in Laos, reflecting broader consensus on species characteristics (Table 5).

3.6. Farmer motivations, preferred tree traits, and constraints to tree management

In Laos, the most frequently cited motivation for planting trees was meeting household needs (40% of respondents), followed by shade (20%), income generation (12%), and supporting livestock production (fodder, fencing; 12%). Environmental motivations, including soil, water, and forest protection, were mentioned by 10% of respondents,

while a smaller proportion cited experimentation, social, or cultural reasons (7%). In Vietnam, the most prominent motivation was income generation (42%); meeting household needs was also important (33%), but less dominant than in Laos. Other motivations were less commonly cited: 10% for soil, water, and forest protection, 7% for shade, and only 1% for supporting livestock production (fodder and fencing). In Laos, the most reported constraint to integrating more trees was a lack of suitable land and competition with other land uses (26%), followed by the availability and quality of seed and seedlings (21%) (Table 6). In Vietnam, the dominant constraint were uncertain economic returns (32%), including yield fluctuations, price volatility and market risks; while pests and diseases were also a significant issue (20%). Individual farmers in both countries mentioned other constraints such as

Table 6

Constraints to integrating more trees on farms (% of mentions by respondents; n = 120 for Laos and 251 for Vietnam). For details on the category 'Other', see Section 3.6 in text.

Constraints	Laos %	Vietnam %
Lack of land	26	11
Seed and seedling availability and quality	21	5
Labour constraints	14	4
Lack of knowledge on growing trees	9	-
Grazing damage	9	3
Financial constraints	8	4
Environmental constraints, species suitability	6	7
Income volatility	-	32
Pests and diseases	-	20
Lack of technology	-	5
Other	7	10

remoteness of farms which made management difficult, problems with fire or weeds, that previously planted trees had died, or that they had only recently started farming.

4. Discussion

Our perception-based assessment of tree species richness and management on smallholder farms in the uplands of the Greater Mekong Subregion reveals that these systems can maintain remarkably high species richness at landscape level (γ -diversity) through land use transitions and serve as potential reservoirs of biodiversity amid broad environmental and socio-economic change (Dawson et al., 2013; Meyfroidt et al., 2013; Appelt et al., 2022; Sun et al., 2026). The perceived tree species richness was higher than that documented in inventory-based studies in agroforestry systems elsewhere in subtropical Asia, where between 93 and 139 species have been observed (Bardhan et al., 2012; Sharma and Vetaas, 2015; Yashmita-Ulman et al., 2021). This was especially notable in Laos, where the perceived species richness even exceeded the species richness documented in protected natural forests (Phomphoumy et al., 2023). Other studies have similarly found that woody species richness in upland agroforestry systems can rival that of natural ecosystems, although with distinct species composition (Scales and Marsden, 2008; Bardhan et al., 2012; Sharma and Vetaas, 2015), demonstrating how human-managed and natural ecosystems complement each other as biodiversity reservoirs. Perception-based assessments may both over- and underestimate actual species richness: farmers might omit species of low cultural salience or may report similar species under a single local name, and comparisons with inventory-based studies should, therefore, be interpreted as indicative of broad patterns and relative differences. Nevertheless, perception-based assessments have been shown to accurately reflect species richness in agroforestry systems where farmers actively manage resources under their direct control (Raneri et al., 2021), supporting the reliability of the patterns reported here.

The presence of unidentified species may have resulted in a slight underestimation of tree species richness in Són La, and to a lesser extent in Lào Cai, but the impact is expected to be minor, as the records were concentrated in one ethnic community and represented a small proportion of all records in Vietnam. Some unidentified species may have referred to identified species reported by other communities under other names, or to non-woody plants which were not included in our analysis.

The rich β -diversity both between landscapes and individual farms indicates that on-farm tree assemblages in the study countries are shaped by both the biogeographic history and sharp topographic and microclimatic gradients of the subregion (de Bruyn et al., 2014), and by the cultural diversity and heterogeneity of land management practices. The contrasting species richness patterns between the countries demonstrate how land use intensity and regeneration dynamics influence the biodiversity potential of smallholder farming systems: Higher α -diversity and lower β -diversity in Laos reflect extensive, low-input

systems that rely heavily on natural regeneration and foster landscape connectivity (Kim and Alounsavath, 2016). In contrast, Vietnam's more commercially oriented systems, established predominantly through tree planting, are not quite as species-rich – but agricultural intensification and tree planting appear to have increased β -diversity, also shown in the number of singleton species and the notable diversity of land uses even on very small farms. Transition from swidden cultivation to other land uses has similarly been observed to lead in dramatic declines in overall plant biodiversity, while potentially enhancing species richness at finer spatial scales (Berkasem et al., 2009). Together, these findings suggest that while agricultural intensification tends to reduce tree species richness maintained through natural regeneration, heterogeneous local knowledge, diverse management decisions, and seed exchange networks boost fine-scale species richness and compositional complexity (Zimmerer et al., 2015; Gbedomon et al., 2017; Le et al., 2021) and potentially help mitigate the negative biodiversity impacts at landscape level (γ -diversity).

The observed differences in land uses were mirrored in the cultural importance of species, which was, in turn, associated with the distribution and depth of knowledge farmers held about the species. In Laos, cultural importance was broadly distributed and associated with multipurpose, naturally regenerating trees, whereas in Vietnam, it was concentrated around a few income-generating species, especially commercially important fruit trees. While farmers in both countries were able to recognize a wide range of ecosystem services provided by trees, similarly to other studies (Nguyen et al., 2020; Khuc et al., 2020), there was a broader consensus of species traits in Vietnam than in Laos. This likely reflects the dominance of planted trees in Vietnam, which require some upfront investment and careful consideration of uses and compatibility with existing land use systems (Lamond et al., 2016). Our findings also support the theory that species valued for their chemical properties (e.g. edible or medicinal uses) may hold greater cultural importance than species valued for physical properties, which are more easily substituted (Guèze et al., 2014). This can result in deeper knowledge of the former species, that extends from their uses to species suitability, growth-related traits, and contribution to other ecosystem services.

The fact that the average species richness per area was roughly twice as high in Laos than in Vietnam across all farm size classes indicates that part of that richness – and the associated local knowledge e.g. of food or forage species – is at risk of being lost with growing market orientation, following similar trajectories as in Vietnam (Scales and Marsden, 2008; Sato et al., 2016). At the same time, conventional intensification has been documented to have the biggest negative impact on species richness on farms managed with medium rather than low intensity (Beckmann et al., 2019), suggesting that risks to biodiversity remain high also in Vietnam. Intensification and preference towards commercially profitable species can further erode functional diversity important for maintaining ecosystem services and increase the vulnerability of both the agroecosystems, and the livelihoods that depend on them, to stressors such as adverse weather or pests and diseases (Castella et al., 2013; Athayde et al., 2015; Nguyen et al., 2020). Tree diversity held in the smallest farms, which were the most species-rich in our study, similar to Ricciardi et al. (2021), may be particularly exposed, and the prevalence of singleton species, especially in Vietnam, further increases the risk of local extinctions and loss of cultural knowledge. Moreover, genetic erosion is a potential concern for species persistence and warrants further investigation in both countries, albeit for different reasons due to regeneration practices: in Laos, continued forest loss and degradation might restrict gene flow to remnant trees on farms, limiting natural regeneration (Dawson et al., 2013; Grandjean et al., 2026); while in Vietnam, genetic bottlenecks might arise from the use of poor quality planting material which is widespread in tree planting efforts (Lengkeek et al., 2005; Jalonen et al., 2018; Bosshard et al., 2021). These are inferred risks based on conservation genetics theory (Reed and Frankham, 2003), reported regeneration patterns, and land-use trends,

rather than molecular analysis, but are highlighted here because genetic diversity is fundamental for species persistence yet rarely considered in farm-level biodiversity assessments (Dawson et al., 2013; Hoban et al., 2023).

The proportion of threatened species recorded in the study areas was much lower than the global average, where approximately 38% of all tree species are considered threatened on the IUCN Red List (BGCI, 2021), but higher than that observed in traditional agroforestry systems in India (Yashmita-Ulman et al., 2021). The relatively low representation of threatened taxa may be partly due to many endangered species being associated with specialized habitats such as lowland dipterocarp forests, limestone karsts, or mangroves, ecosystems that are underrepresented in community landscapes and agroforestry systems (Sodhi et al., 2010; Zhu et al., 2023). However, in Laos, our survey found a relatively common presence of some globally threatened species, suggesting that agricultural landscapes can play an important conservation role for threatened trees – provided that adequate genetic diversity can be maintained through land use transitions (Dawson et al., 2013; Grandjean et al., 2026).

Our results showed that farmers' preferences and opportunities to maintain and increase tree cover and species richness on farms are shaped by a mix of motivations such as livelihood security, income generation, and ecosystem services – with subsistence uses again emphasized in Laos and commercial uses in Vietnam. Interestingly, land availability was the most pressing constraint to tree planting in Laos, but not in Vietnam, despite the much smaller farm sizes there. This highlights the importance of tenure security in fostering smallholder investments in tree planting and management. Customary tenure practices, including swidden cultivation and communal forest management, have historically provided both subsistence and cultural identity in Laos, but these systems have been increasingly undermined by land allocation programs, conservation initiatives, and commercial concessions (Thongmanivong and Fujita, 2006; Baird, 2017). With the relatively more secure land tenure and more intensive land uses in the study area in Vietnam, farmers' concerns shifted from land to market and production risks such as market volatility, unreliable contracts, and pest pressures, mirroring patterns in agroforestry and perennial crop studies (Hoang et al., 2023; Crowther et al., 2020; Khuc et al., 2020).

Strengthening tree diversity management in agricultural mosaics requires protecting remaining forests (Sodhi et al., 2010; Sun et al., 2026), integrating native and multifunctional tree species into commercial production systems to sustain ecological and cultural values (Nguyen et al., 2020), promoting knowledge exchange among farmers about species and management practices (Zimmer et al., 2022), and considering the diverse social and cultural norms that affect tree planting decisions among ethnic groups (Nguyen et al., 2021). Farmers' recognition of the environmental values of trees for soil, water and biodiversity conservation can serve as an entry point and guide interventions that align conservation, livelihoods and climate resilience. Agroforestry offers opportunities to build on local knowledge of swidden agriculture and resource management (Son et al., 2019; van Der Meer Simo et al., 2020), but constraints to its wider adoption, such as tenure security and land rights (Arvola et al., 2020), limited access to markets, market information, and technical and financial support (Do and Mulia, 2018; Do et al., 2020; Ferrer et al., 2023), must first be addressed. Synergies exist: positive market prospects and government subsidies can counteract negative perceptions of land tenure security and encourage tree planting (Hoang et al., 2023). Limited access to quality planting material, also reported elsewhere in Asia (Bossard et al., 2021), highlights the need for investments in seed systems to ensure the persistence of native species in production landscapes as exotic commodities become more prevalent. At the same time, our findings demonstrate the critical role of natural regeneration in sustaining native tree diversity especially in extensively managed farming systems and systems undergoing intensification – calling for policies and practices that protect regenerants and reduce pressures such as fire and

grazing in such systems *during* and not only after transitions to facilitate biodiversity recovery (Chazdon et al., 2020).

Our findings on the high compositional turnover, the depth of local knowledge documented, the number of unidentified species managed by ethnic minority groups in Vietnam, and the high proportion of species not assessed for their conservation status, highlight the need for further botanical assessment and ethnobotanical research in the Greater Mekong subregion. Despite substantial existing botanical work, greater attention is required to systematically document local and indigenous knowledge systems regarding tree species (ethnospices) across different cultural groups, particularly in agricultural mosaic landscapes undergoing rapid transformations. Further studies could also assess the impact of respondent age on perceived species richness and local extinctions over time.

5. Conclusion

Our study demonstrates that smallholder farming landscapes in northern Laos and Vietnam can harbour unexpectedly high tree species richness, shaped by contrasting land use histories, management intensities, and cultural values. As the study was perception-based and employed purposive sampling of farming households with history of integrating trees on their farms, the findings characterize the range of potential tree species richness and local knowledge rather than representing average farming contexts across the subregion. Nonetheless, these findings highlight agricultural mosaics as potentially important contexts for biodiversity and associated local knowledge, and point to several priorities for policy and management of on-farm tree diversity: (1) Supporting the integration and conservation of native trees, particularly food and medicinal species in which local communities hold deep expertise, in commercial production systems and emerging agroecological and agroecotourism models, through local policy and financial frameworks, (2) Strengthening seed systems and knowledge transmission by mapping seed sources and exchange networks, and establishing local production and distribution networks for quality native tree seed, (3) Developing accessible databases of tree species distributions, uses, management practices and propagation techniques to support farmer decision-making. These priorities are urgent both in Vietnam, where land use intensification appears to have already narrowed species richness and concentrated traditional knowledge around commercial species, and in Laos, where the remaining high naturally regenerating tree diversity needs to be safeguarded during continued land use intensification. Future work should examine genetic diversity and regeneration processes in farm landscapes and explore how farmer-led innovations can sustain multifunctional tree assemblages under accelerating environmental and socioeconomic change.

CRedit authorship contribution statement

Riina Jalonen: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing. **Dunja Mijatovic:** Data curation, Formal analysis, Writing – original draft. **Tobias Fremout:** Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Le Viet Dung:** Data curation, Investigation, Project administration, Writing – review & editing. **Simone Vongkhamho:** Data curation, Investigation, Project administration, Writing – review & editing. **Chaloun Bounithiphonh:** Data curation, Investigation, Writing – review & editing. **Bounthavy Chalernsouk:** Data curation, Investigation. **Nout Xaypheng:** Data curation, Investigation. **Emmy Ling Ling Goh:** Formal analysis, Writing – review & editing. **Hannes Gaisberger:** Formal analysis, Visualization, Writing – review & editing. **Luu Ngoc Quyen:** Supervision.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Riina Jalonen reports financial support was provided by CGIAR Trust Fund. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Ms Phonepakai Phongoudome and Mr Somsack Chanthavong from the National Agriculture and Forest Research Institute of Lao PDR, and all staff of the Northern Mountainous Agriculture and Forestry Science Institute (NOMAFSI), Vietnam, who contributed to data collection. We would also like to thank all participating farmers for their time. This work was carried out under the CGIAR Multifunctional Landscapes Program and Sustainable Farming Program. We would like to thank all funders who supported this research through their contributions to the CGIAR Trust Fund (www.cgiar.org/funders).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.tfp.2026.101365](https://doi.org/10.1016/j.tfp.2026.101365).

Data availability

Data will be made available on request.

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