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# Biodiversity in silvopastoral systems: A global review and meta-analysis

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ABSTRACT

Understanding the biodiversity values of silvopastoral systems (SPS) is crucial to developing ecologically sustainable grazing systems that can integrate production and conservation goals. Nevertheless, the understanding of how effectively SPS enhance biodiversity compared to other land use systems remains limited. A global systematic review was conducted using 253 publications to identify knowledge gaps in biodiversity research in SPS. Additionally, a meta-analysis was carried out using 730 comparisons from 78 publications to quantify the effect of SPS on biodiversity compared to their references, including open pastures and ungrazed forests. The results highlight the need for further biodiversity research on vertebrates and microbes across SPS types, particularly systems with planted trees or shrubs in underrepresented regions. The meta-analysis showed that the effect of SPS on biodiversity compared to their references varied with system types and taxonomic groups. SPS supported 28.4% higher biodiversity than open pastures. SPS with native (unplanted) and planted trees both increased biodiversity relative to open pastures by 36.3% and 20.9%, respectively. However, SPS with native trees had 18.1% lower biodiversity than native forests. At the taxa level, native tree-based SPS exhibited similar biodiversity of birds, but lower levels of plants and invertebrates relative to native forests. In contrast, these native systems enhanced invertebrate communities compared to open pastures. These findings suggest that transitioning from open grazing systems to SPS represents a promising strategy to enhance biodiversity. Furthermore, establishing SPS with native trees serves as a complementary approach to biodiversity conservation, rather than a direct substitute for native forests.

## 1. Introduction

Silvopastoral systems (SPS) are land-use practices that intentionally combine trees or shrubs and livestock within the same land area (Nair, 1991). SPS typically capture the advantages of shade and forage for livestock production, while also providing timber or biomass products. Agrosilvopastoral systems, a broader category of SPS, incorporate crops in addition to trees or shrubs and livestock, increasing production streams and management complexity. In this study, the term SPS refers to both silvopastoral and agrosilvopastoral systems, acknowledging that these two systems are often used interchangeably in the literature, particularly where crops are introduced during the initial establishment phase, and the system later develops into SPS, or where crop–livestock rotations are integrated within the system.

SPS are increasingly recognised as ecologically sustainable alternatives to open grazing practices, offering a multifunctional land-use approach. Beyond their capacity to diversify income streams through multiple products such as livestock, timber, biomass or carbon (Jose and Dollinger, 2019; Francis et al., 2022), SPS can improve animal welfare by providing shade, shelter, and more favourable thermal conditions under tree canopy cover (Mancera et al., 2018; Lemes et al., 2021). They also contribute to improving microclimatic conditions, reducing heat stress (Schinato et al., 2023), while simultaneously increasing soil carbon stocks and biomass-based carbon sequestration, thereby offsetting greenhouse gas emissions from livestock grazing and supporting climate-change mitigation goals (Que et al., 2022; Torres et al., 2023). In addition, incorporating trees into grazing lands can provide the potential to restore degraded landscapes (Kumar et al., 2022; Baradwal et al., 2023) by preventing soil erosion (Mackay-Smith et al., 2025) and enhancing soil quality (Poudel et al., 2022).

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Importantly, these systems have demonstrated the potential to enhance biodiversity of taxonomic groups such as birds and ground invertebrates by increasing habitat heterogeneity and structural complexity compared to open grazing systems (Bagella et al., 2020; Giraldo et al., 2024). However, their biodiversity values might not replicate those of ungrazed natural forests and woodlands (McDermott et al., 2015; Montoya-Molina et al., 2016; Duque-Vélez et al., 2022).

Recently, the global emphasis on the biodiversity benefits of SPS has been underpinned by extensive studies that reported taxonomic diversity of flora and fauna in these systems in the literature. However, there is a lack of a comprehensive and systematic understanding of how effectively SPS enhance biodiversity compared to other land use systems. The existing evidence remains scattered and often contradictory because the effect of SPS on biodiversity might differ with different system types and taxonomic groups. For instance, SPS supported significantly greater levels of bird species richness (McAdam et al., 2007) and abundance (Giraldo et al., 2024), bacteria abundance (Xu et al., 2017) and diversity (Barros et al., 2021), plant species richness (Bagella et al., 2020) and abundance (Giraldo et al., 2024), dung beetle species richness (Alonso et al., 2019) and diversity (Duque-Vélez et al., 2022), and ant species richness (Gaytán et al., 2021) than open pastures. In contrast, Veríssimo et al. (2021) found a higher abundance of flying insects, Kinneen et al. (2023) recorded a higher abundance of Hemiptera species, and Mackay-Smith et al. (2023) observed a higher plant diversity in open pastures than in SPS. Other studies found no significant difference between these land use systems in plant (Clavijo et al., 2005; Orefice et al., 2017) and dung beetle richness (Lopes et al., 2020; Alonso et al., 2021).

Compared to native forests, SPS with native (unplanted) trees had lower bird richness (Mastrangelo and Gavin, 2012; McDermott et al., 2015), reduced levels of plant richness (Mancilla-Leytón et al., 2013; Bagella et al., 2020), soil invertebrate diversity (Rousseau et al., 2013), and dung beetle abundance and richness (Montoya-Molina et al., 2016). In contrast, several studies found SPS with native trees supported higher invertebrate richness than native forests; for example, earthworms (Gudeta et al., 2022) and dung beetles (Gómez-Cifuentes et al., 2019), while other research reported no significant difference in dung beetle (Alonso et al., 2019, 2021) and bird diversity (Edo et al., 2024) between these two habitats. Relative to planted forests, SPS with planted trees supported higher species richness of herbaceous native plants (Demeter et al., 2021) and ground beetles (Nanni et al., 2021), and greater microbial abundance and diversity (López-Ramírez et al., 2023), while these planted systems reduced the species richness of plants (Six et al., 2016) and ground-dwelling arthropods (Nanni et al., 2022).

However, the literature usually reports single taxonomic groups (e.g., plants or birds), while the biodiversity values of SPS should be evaluated across multiple taxa to provide a comprehensive understanding of their potential for biodiversity conservation. In addition, extensive studies often assessed the biodiversity value of SPS using simple basic metrics of abundance or species richness. However, biodiversity extends beyond those assessments and can be more truly evaluated using a mix of complex biodiversity indices, including Shannon and Simpson diversity or Hill estimates (Hsieh et al., 2016). Therefore, it is challenging to draw a general conclusion on how SPS affect overall biodiversity compared to open pastures and ungrazed forests. Furthermore, the contrasting effects of SPS compared to their references vary across system types that likely reflect how SPS are established and managed for different purposes (Gómez-Cifuentes et al., 2019; de Macêdo Carvalho et al., 2024). SPS with native trees are usually established in open natural woodlands, mainly for livestock and/or biomass production with low management levels. For example, oak woodland-based silvopastoral practices are common in Spain and Portugal (Rodríguez-Rojo et al., 2022). In contrast, SPS with planted trees often integrate woody and pasture species in an intentional, intensive and interactive way for multiple production purposes (Jose and Dollinger, 2019). For example, SPS with pines and eucalypts in some Latin American countries (Peri et al., 2016).

Therefore, this study conducted a global review of biodiversity research in SPS and a meta-analysis on the effect of SPS on overall biodiversity and the effect of different SPS types on the biodiversity of taxonomic groups. This systematic review aims to identify biodiversity research trends in SPS, while the meta-analysis will provide a comprehensive understanding of how effectively SPS enhance biodiversity compared to open pastures and ungrazed forests. The findings of this study are crucial for promoting the development of ecologically sustainable livestock production systems that can balance production and biodiversity conservation goals.

## 2. Materials and methods

### 2.1. Databases and search terms

Scopus (developed by Elsevier) and Web of Science (developed by Thomson Scientific) were used to search by TOPIC for biodiversity-related publications in SPS. To be included in our database, the targeted publications must mention two components: SPS and biodiversity. We used SPS-related search terms such as *silvopast* OR silvo-past* OR silvipast* OR silvi-past* OR agroforest* OR agro-forest* OR agro-silvo* OR agrosilvo* OR agro-silvi* OR agrosilvi* OR horti-silvi-pastur* OR "woody pasture*" OR pasture-tree* OR tree-pasture* OR "pasture with tree*" OR "shaded pasture*" OR livestock–tree* OR tree-livestock OR "tree-based grazing" OR "grazed woodland*" OR "grazed forest*" OR "grazed plantation*"* and biodiversity-related search terms including *diversity OR biodiversity OR richness OR abundance OR evenness OR composition OR conservation* to select biodiversity-related publications in SPS. This search was conducted in August 2024 and refined to articles written in English, resulting in 2733 records from Scopus and 2376 records from Web of Science.

### 2.2. Criteria and study selection

We included only English-written publications that studied taxonomic groups in SPS and excluded those in ungrazed agroforestry systems that did not compare their biodiversity with SPS. To ensure relevance to our research objectives, publications were only retained if they reported biodiversity metrics such as composition, abundance, richness, diversity index, and evenness. Publications addressing non-relevant topics (e.g., carbon estimation, tree growth, animal welfare, pasture and livestock productivity) were excluded. The screening and selection of relevant publications followed the PRISMA 2020 protocol (Page et al., 2021) (Fig. 1).

### 2.3. Systematic review

A total of 253 publications that met the criteria for systematic review were selected (Supplementary Table A.1). The trends in biodiversity-related publications in SPS were quantitatively analysed by year and country. Subsequently, the number of studies was summarised according to different SPS types including: (1) SPS with native (unplanted) trees, (2) SPS with planted trees, and (3) SPS with planted shrubs; taxonomic groups (plant, invertebrate, bird, mammal, reptile, amphibian, and microbe); and biodiversity metrics (composition, abundance, richness, diversity, and evenness). The number of studies might be higher than the number of publications because some publications reported more than one SPS type, taxonomic group or biodiversity metric. Additionally, trends in the comparison of taxonomic groups and biodiversity metrics among SPS, open pastures, and ungrazed forests were analysed. Open pastures referred to grazed open pastures or grasslands, often located adjacent to SPS. Ungrazed forests encompassed both native (unplanted) and planted forests. Native forests were characterised by different restoration histories and conditions across regions, ranging from secondary to primary forests, young to old

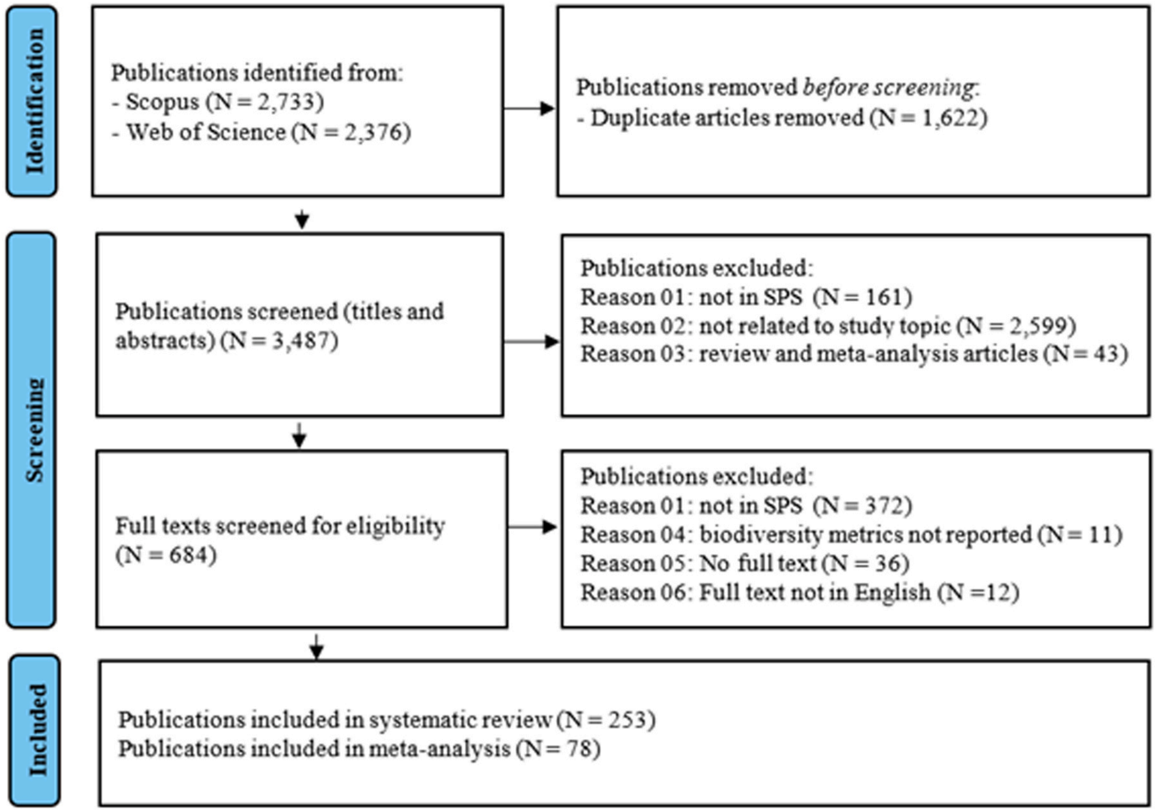


**Fig. 1.** PRISMA 2020 flow diagram for systematic reviews.

regrowth forests, and open woodlands to dense forests. Critical patterns of these native habitats, such as species, density, forest age, patch size, and vegetation composition, were not often widely reported in selected publications. Similarly, these features were insufficiently described for SPS established within native forests or woodlands. Therefore, we combined a wide range of native forests as a reference to compare with SPS with native trees. SPS with planted trees and planted forests also varied with species, tree age and density, and silvicultural practices across publications. However, planted forests often used the same tree species and age as SPS with planted trees, but with higher tree stockings than these systems in the same publications.

### 2.4. Data extraction

Of the 253 publications selected, 121 were excluded, including publications that studied biodiversity within SPS (including under and outside trees in the same system) or compared among SPS without references (hereafter referred to as SPS only), and 132 compared biodiversity metrics between SPS versus open pastures and/or SPS versus ungrazed forests were retained. Of these, 78 publications that reported sample size (*n*), mean (*m*), and either standard deviation (*sd*) or standard error (*se*) were included for data extraction (Supplementary Table A.2). Data were extracted from tables and graphs in the publications using Web Plot Digitizer (Rohatgi, 2011). If a *se* was presented, it was converted to *sd*. The metadata were then grouped by different SPS types, taxonomic groups, and biodiversity metrics to create data subsets for the meta-analysis. For biodiversity subsets, all comparisons of biodiversity metrics across seven taxonomic groups were pooled, while all comparisons of biodiversity metrics of each group were pooled for taxonomic subsets. All subsets were then grouped by different comparison types between SPS types and their references. For example, the "Biodiversity_SPS vs OP" subset was created to assess the effect of SPS on overall biodiversity relative to open pastures, "Bird_SPS_n vs NF" subset was made to evaluate the effect of SPS with native trees on bird biodiversity relative to ungrazed native forests, and "Richness_SPS_n vs NF" was created to test the effect of SPS with native trees on species richness compared to ungrazed native forests. The number of publications (N) and the number of comparisons (K) were calculated for each data subset. Although meta-analyses can be performed with a small number of publications (fewer than 10), increasing the number of included publications substantially improves statistical power and the reliability of results (Borenstein et al., 2009; Chandler et al., 2019). Therefore, to ensure robust inference, only data subsets with $N \geq 10$ and $K \geq 30$ were included in the meta-analysis. A total of 730 comparisons (Supplementary Table A.3) and 89 data subsets (Supplementary Table A.4) were extracted from 78 publications.

### 2.5. Meta-analysis

In meta-analyses, effect sizes are commonly estimated using either the log response ratio (ln *RR*) or the standardised mean difference (*SMD*). The ln *RR*, calculated as the natural logarithm of the ratio of means, is frequently applied in ecological meta-analyses due to its lower bias in studies with small sample sizes ($n < 10$), while the *SMD* is typically calculated using Cohen's *d* or Hedges' *g*, which are more susceptible to bias when sample sizes are small (Hedges et al., 1999; Nakagawa et al., 2015). In this study, effect sizes were calculated following the methods described by Hedges et al. (1999), as outlined below:

$$\ln RR = \ln(m_t) - \ln(m_c) = \ln(m_t / m_c) \tag{1}$$

$$\mathrm{var}(\ln RR) = sd_t^2/n_t\, m_t^2 + sd_c^2/n_c\, m_c^2 \tag{2}$$

where: ln *RR* is the log response ratio (effect size) of the treatment (*t*) relative to the control (*c*), *var (*ln *RR)* is the variance of ln *RR*, *m* is the mean value, *n* is the sample size, and *sd* is the standard deviation.

Before testing effect sizes, Cochran's Q test of heterogeneity (Q) was performed to decide whether to use fixed or random effect models. All selected 11 data subsets exhibited significant heterogeneity ($p < 0.001$). Therefore, multilevel random-effect models were fitted using the "rma.mv' function with restricted maximum likelihood (REML) estimation. In all models, a random effect structure of effect size nested within publication was included to account for the nonindependence of multiple effect sizes in the same publications and to model heterogeneity between and within publications (Viechtbauer, 2007). Meta-analysis was performed in R version 4.4.1 (R Core Team, 2022) using the "metafor" package (Viechtbauer, 2010). Variance components were extracted from REML models to quantify the distribution of heterogeneity of effect sizes within and between publications. For each subset, the mean log response ratio (ln RR) was estimated, and the percentage change (%) was calculated using equation [3].

$$\% \text{ Change} = (e^{\ln RR} - 1) \times 100\% \tag{3}$$

## 3. Results

### 3.1. Trends of biodiversity studies in silvopastoral systems

A total of 253 biodiversity-related publications on SPS were selected across 41 countries between 1980 and 2024 (Fig. 2). The number of publications on this topic has significantly increased since 2000, particularly in the last decade. The distribution of SPS biodiversity research was uneven across geographic regions. European and South American countries accounted for 69.2% (N = 175) of the total publications. Europe contributed 36.4% (N = 92), followed by South America (N = 83; 32.8%), North America (N = 27; 10.7%), and Central America (N = 14; 5.5%). In Europe, Spain (N = 30) and Portugal (N = 25) together contributed 59.8% of European publications, while Brazil (N = 26), Colombia (N = 24), and Argentina (N = 22) were the leading countries in South America, accounting for 86.7% of publications in this region. In contrast, biodiversity in SPS was less studied in Oceania (N = 13; 5.1%), Asia (N = 12; 4.7%), and Africa (N = 8; 3.2%).

Among SPS types, SPS with native trees attracted the most research attention (193 studies, 74.5% of 259 studies), followed by SPS with planted trees (50; 19.3%), and SPS with shrubs (16; 6.2%) (Table 1). Among comparison types, 121 studies (41.2% of 294 studies) assessed biodiversity within SPS without reference to open pastures or ungrazed

**Table 1**
Number of studies according to different silvopastoral system (SPS) types, comparisons, taxonomic groups, and biodiversity metrics.

| Category | Classification | Total number of studies | Number of studies (%) |
|---|---|---|---|
| SPS type | SPS with native trees | 259 | 193 (74.5) |
| | SPS with planted trees | | 50 (19.3) |
| | SPS with shrubs | | 16 (6.2) |
| Comparison type | SPS only | 294 | 121 (41.2) |
| | SPS and ungrazed forests | | 98 (33.3) |
| | SPS and open pastures | | 75 (25.5) |
| Taxonomic group | Plant | 273 | 117 (42.9) |
| | Invertebrate | | 76 (27.8) |
| | Bird | | 32 (11.7) |
| | Microbe | | 23 (8.4) |
| | Mammal | | 18 (6.6) |
| | Reptile | | 5 (1.8) |
| | Amphibian | | 2 (0.7) |
| Biodiversity metric | Richness | 600 | 173 (28.8) |
| | Abundance | | 155 (25.8) |
| | Composition | | 130 (21.7) |
| | Diversity index | | 113 (18.8) |
| | Evenness | | 29 (4.8) |

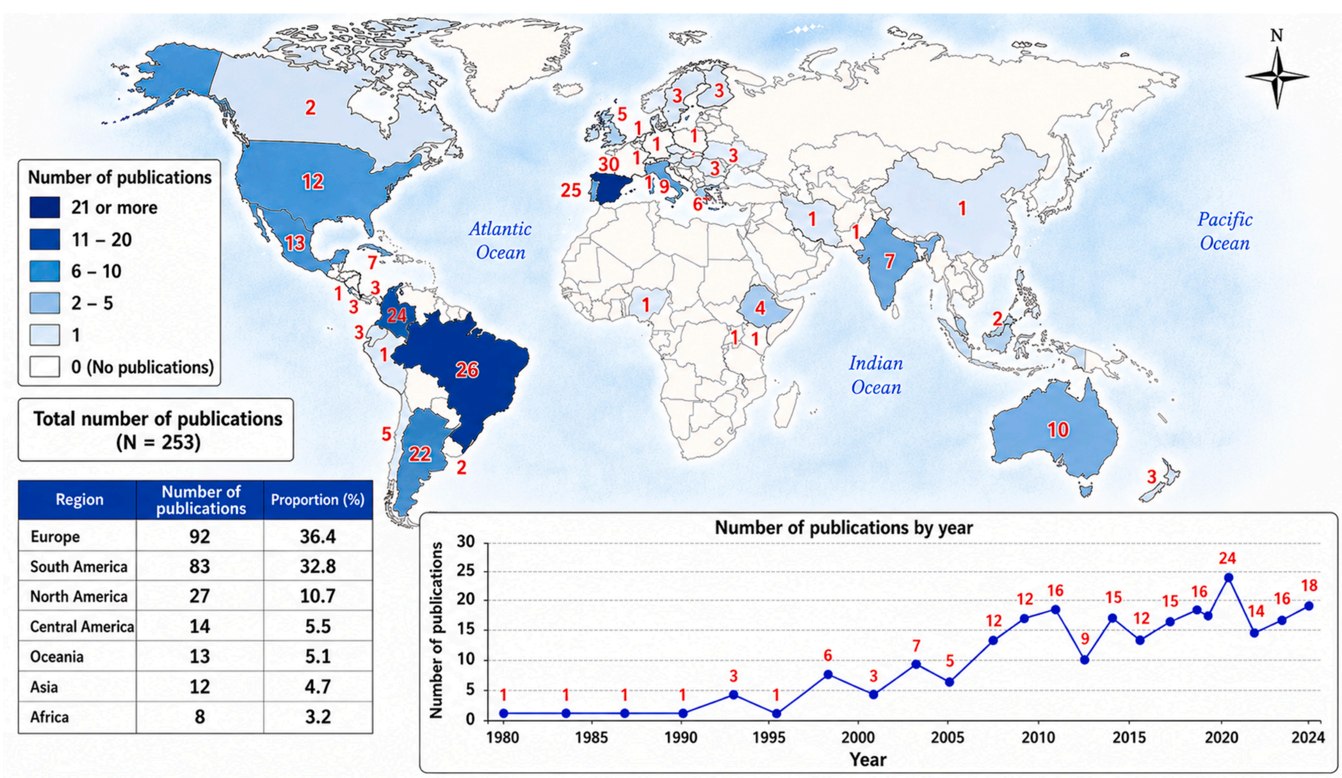


**Fig. 2.** Temporal and geographic distribution of biodiversity publications in silvopastoral systems. The figure was created using QGIS and ChatGPT (OpenAI), based on the data summarised from 253 publications. Five publications conducted across multiple countries were excluded from the publication distribution by country and region.

forests, whereas 98 (33.3%) compared biodiversity metrics between SPS and ungrazed forests and 75 (25.5%) compared those between SPS and open pastures. Across taxonomic groups, plants were the most frequently studied group (117 studies; 42.9% of 273 studies), followed by invertebrates (76; 27.8%), birds (32; 11.7%), microbes (23; 8.4%), and mammals (18; 6.6%). In contrast, reptiles and amphibians received relatively limited attention, 5 and 2 studies, respectively. Among biodiversity metrics, richness had the highest number of studies (173; 28.8% of 600 studies), followed by abundance (155; 25.8%), composition (130; 21.7%), diversity index (113; 18.8%), and evenness (29; 4.8%).

Across seven taxonomic groups, research effort in SPS with native trees was substantially greater than in SPS with planted trees and SPS with shrubs (Fig. 3A). Plant biodiversity within SPS with native trees received the greatest research attention, accounting for 92 studies (76.7% of plant studies), compared with 26 studies (21.7%) in SPS with planted trees and only 2 studies (1.6%) in SPS with shrubs. Plants and invertebrates were the most extensively studied taxonomic group, consistently showing the highest numbers of studies across all metrics (Fig. 3B). Plant studies predominantly measured richness (88 studies), followed by composition (76), diversity index (56) and abundance (52), whereas invertebrate research most frequently examined abundance (60) and richness (56).

Comparisons between SPS and reference systems varied across SPS types (Fig. 3C). Comparisons between SPS and open pastures (47 studies) were considerably less represented than those of SPS and ungrazed forests (83), while comparisons between SPS and ungrazed forests were more frequent in SPS with planted trees (23). Research interest in comparing SPS with their references also differed among taxonomic groups (Fig. 3D). For plants, 65 studies were carried out in SPS only, 39 compared SPS and ungrazed forests, and 24 compared SPS and open pastures, whereas 36 invertebrate studies compared SPS and ungrazed forests, 35 compared SPS and open pastures, and 26 were conducted without reference systems.

### 3.2. Overview of metadata

A total of 730 comparisons were included in the meta-analysis, comprising 532 comparisons (72.9%) extracted from 53 publications on SPS with native trees, 162 (22.2%) from 22 publications on SPS with planted trees, and 36 (4.9%) from 4 publications on SPS with shrubs (Appendix Table A.1). Among taxonomic groups, invertebrates contributed the largest proportion of the metadata, representing 286 comparisons (39.2%) from 35 publications, followed by birds with 257 comparisons (35.2%) from 13 publications and plants with 127 comparisons (17.4%), whereas other groups accounted for only 8% of the metadata. Across studied metrics, richness and abundance, which together represent the largest contribution of the metadata (38.4% and 36.8%, respectively), are substantially greater than diversity index (19.3%) and evenness (5.5%). SPS with native trees versus native forests were the most frequently compared, contributing 52.5% of the metadata, followed by SPS with native trees versus open pastures (20%) and SPS with planted trees versus open pastures (14.4%).

System features of SPS with planted trees, such as tree species, density, and age, were extracted from 22 publications (Supplementary Table A.5), whereas these attributes of SPS with native trees were not widely reported. SPS with planted trees used a variety of tree species, mainly *Pinus sp.*, *Eucalyptus sp.*, *Populus sp.*, and *Acacia sp.* In these systems, tree density averaged at 509 trees $ha^{-1}$ and ranged from 100 to 2500 trees $ha^{-1}$. Most publications (75%) reported SPS densities between 200 and 600 trees $ha^{-1}$. The tree age had an average of 11.3 years and a range from 2 to 25 years. More than half of the publications (55%) were carried out in systems older than 10 years, and 40% had the tree age between 5 and 10 years.

The metadata contained 11 subsets that met the criteria of $N \geq 10$ and $K \geq 30$ and were tested for their heterogeneity and meta-analysis. All subsets exhibited significant heterogeneity among effect sizes (Table 2), with the percentage of heterogeneity ($I^2$) values greater than 90% ($p < 0.0001$). The heterogeneity between and within publications

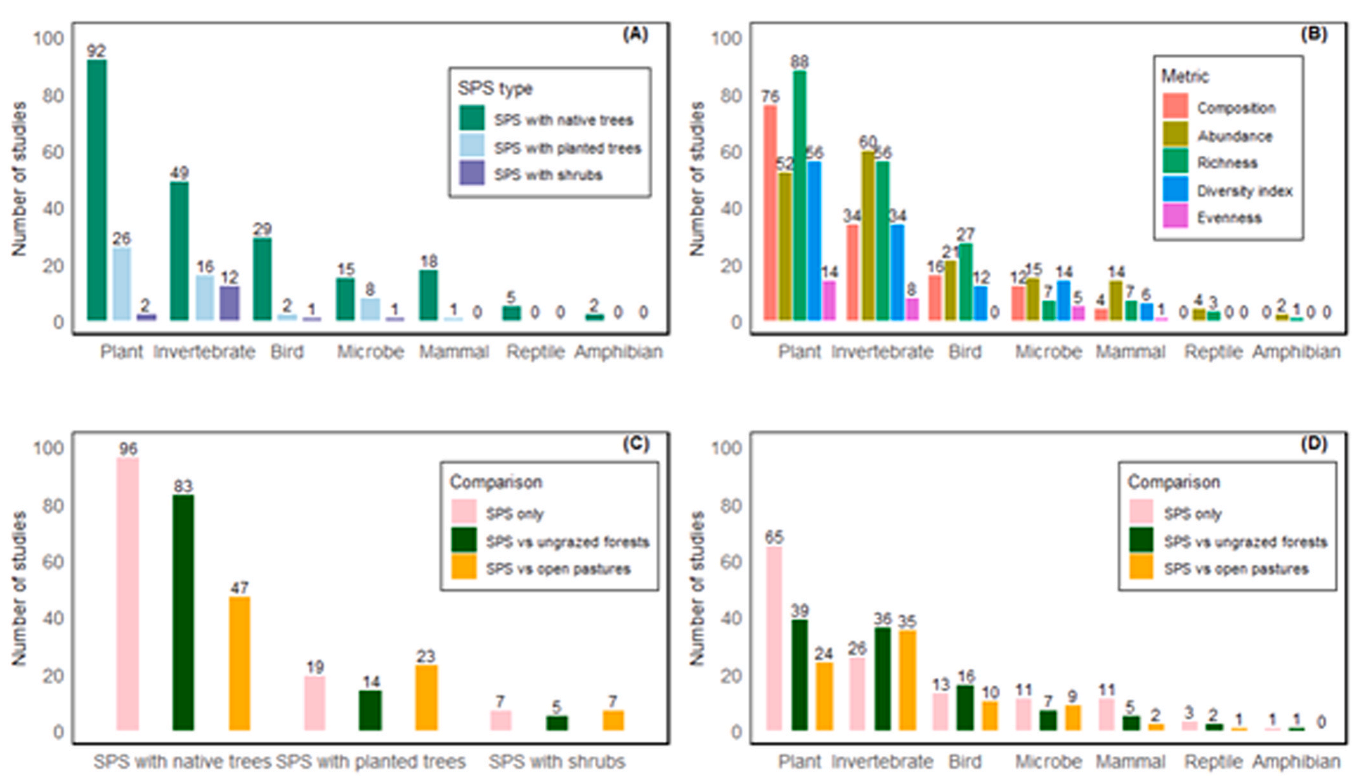


**Fig. 3.** Number of studies according to: taxonomic groups in silvopastoral systems (SPS) types (A), biodiversity metrics of taxonomic groups (B), comparisons of SPS types (C), and comparisons across taxonomic groups (D).

**Table 2**
Heterogeneity tests and meta-analysis results of 11 selected data subsets.

| Subset | N | K | Heterogeneity | | | REML | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Q | $I^2$ | Sig | ln *RR* | SE | p value | Sig | % change |
| Biodiversity_SPS vs OP | 47 | 279 | 74427 | 99.6 | *** | 0.25 | 0.08 | 0.002 | ** | 28.4 |
| Biodiversity_SPS_n vs OP | 26 | 146 | 16074 | 99.1 | *** | 0.31 | 0.13 | 0.02 | * | 36.3 |
| Biodiversity_SPS_n vs NF | 45 | 383 | 39759 | 99.0 | *** | −0.2 | 0.06 | 0.001 | *** | −18.1 |
| Biodiversity_SPS_p vs OP | 18 | 105 | 54450 | 99.8 | *** | 0.19 | 0.08 | 0.02 | * | 20.9 |
| Plant_SPS_n vs NF | 16 | 74 | 4218 | 98.3 | *** | −0.16 | 0.07 | 0.02 | * | −14.8 |
| Bird_SPS_n vs NF | 11 | 183 | 1994 | 90.9 | *** | −0.08 | 0.11 | 0.46 | ns | −7.7 |
| Bird richness_SPS_n vs NF | 11 | 98 | 1066 | 90.9 | *** | −0.08 | 0.10 | 0.40 | ns | −7.7 |
| Invertebrate_SPS_n vs OP | 16 | 61 | 10655 | 99.4 | *** | 0.43 | 0.17 | 0.01 | * | 53.7 |
| Invertebrate_SPS_n vs NF | 18 | 109 | 14996 | 99.3 | *** | −0.28 | 0.12 | 0.02 | * | −24.4 |
| Invertebrate abundance_SPS_n vs OP | 13 | 30 | 8534 | 99.7 | *** | 0.47 | 0.28 | 0.09 | ns | 60 |
| Invertebrate abundance_SPS_n vs NF | 15 | 56 | 13898 | 99.6 | *** | −0.36 | 0.16 | 0.03 | * | −30.2 |

*Notes:* N = number of publications, K = number of comparisons, Q = Cochran's heterogeneity tests, ln RR is the log response ratio (effect size), and SE is standard error. REML = Restricted Maximum Likelihood, $I^2$ = percentage of heterogeneity, SPS = Silvopastoral systems, OP = Open pastures, SPS_n = SPS with native trees, SPS_p = SPS with planted trees, NF = Native forests. Statistical significance is denoted as ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and ns (not significant).

was distributed relatively evenly in most biodiversity subsets (Appendix Table A.2), particularly for SPS versus open pastures (55% vs 45%) and SPS with native trees versus native forests (51% vs 49%). In contrast, heterogeneity in bird subsets was driven primarily by differences among publications (71–74%), whereas subsets of plants (74%), invertebrates (57%−72%), and SPS with planted trees (75%) were dominated by within publication variation.

### 3.3. *Effect of SPS on biodiversity*

The meta-analysis revealed that the effect size of SPS on biodiversity compared to their references varied across SPS types and taxonomic groups (Fig. 4). SPS increased biodiversity by 28.4% relative to OP (p = 0.002) (Table 2, Fig. 4). SPS with native trees showed a 36.3% increase in biodiversity (p = 0.02), whereas SPS with planted trees enhanced this value by 20.9% (p = 0.02) compared to open pastures. Compared to native forests, biodiversity in SPS with native trees was 18.1% lower (p = 0.002).

The effect size of SPS on biodiversity compared to their references also varied across taxonomic groups. SPS with native trees exhibited lower biodiversity relative to native forests, with reductions of 7.7% in birds, 14.8% in plants, and 24.4% in invertebrates. However, bird biodiversity in SPS with native trees did not statistically significantly differ from ungrazed native forests (p = 0.46), particularly this group showed a similar species richness between these two systems (p = 0.40). In contrast, SPS with native trees substantially increased invertebrate biodiversity by 53.7% relative to open pastures. No significant difference in invertebrate abundance was detected among SPS with native trees and open pastures (p = 0.09), while native forests increased the abundance of this group by 32.2% (p = 0.03) relative to this SPS.

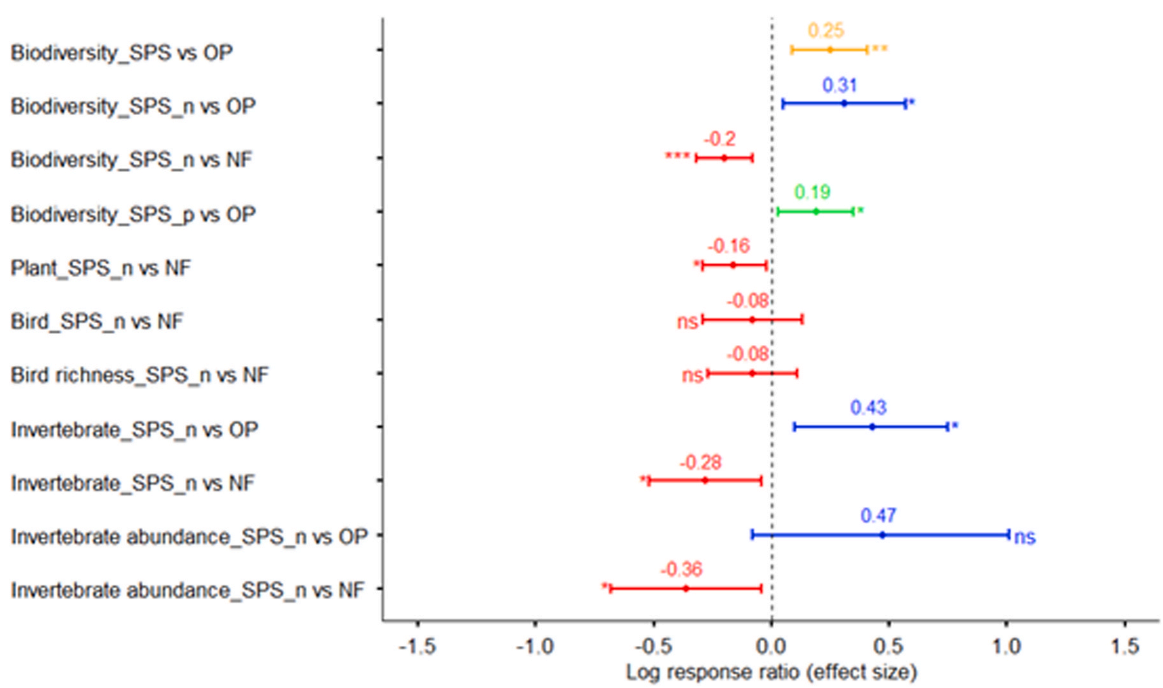


**Fig. 4.** Log response ratio (effect size) of silvopastoral systems (SPS) on biodiversity. SPS types include: SPS with native trees (SPS_n) and SPS with planted trees (SPS_p). Reference systems include: open pastures (OP) and native forests (NF). Points represent effect size means, and lines show the 95% confidence interval. Statistical significance is denoted as ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and ns (not significant). Colours represent comparisons: SPS versus OP (orange), SPS_n versus OP (blue), SPS_n versus NF (red), and SPS_p versus OP (green).

## 4. Discussion

### 4.1. Trends of biodiversity research in silvopastoral systems

The observed rise in biodiversity-related publications on SPS over the past decade reflects growing global recognition of their potential to enhance ecological services in agricultural landscapes (Jose and Dollinger, 2019; Smith et al., 2022). The uneven geographic distribution of these publications likely reflects disparities in research interests, funding availability, and availability of SPS trials. In addition, this is likely due to the exclusion of non-English written publications in some countries, such as China and Russia. The large contribution (nearly 70%) in Europe and South America likely reflects the long history of landscape silvopastures and the recent trend of intensive SPS, where livestock was purposefully integrated with forested systems to support production and ecosystem services (Cubbage et al., 2012; Peri et al., 2016). Conversely, Africa, Asia, and Oceania remain significantly underrepresented, likely due to limited adoption of SPS, driven by multiple factors, including lack of knowledge and demonstration of SPS benefits, high establishment costs, low public and institutional emphasis on tree-livestock integration, and ecological constraints such as low rainfall and fire risks. For example, Australia has a long history of extensive rangeland grazing systems and land clearing for grazing (Reside et al., 2017; Hacker et al., 2020), while various barriers impede the development of SPS (Fleming et al., 2019). Another example, New Zealand, a pioneer in the study of SPS among temperate countries, with the early adoption of SPS with poplar (*Populus spp.*) and willow (*Salix spp.*) for grazing and soil protection. However, this country had similar barriers for the wide adoption of these systems (Mackay-Smith et al., 2025). To better understand the biodiversity benefits of SPS across different contexts, there is a need for further studies in underrepresented regions, especially in countries where landholders are facing challenges related to land-use management and biodiversity conservation. For example, in northern Australia, clearing land for livestock production was a major threat to biodiversity (Neldner et al., 2017; Reside et al., 2017), while large areas of unmanaged native forests are grazed by cattle, characterised by poor timber production and quality (Lewis et al., 2022).

Despite the increasing volume of research, significant knowledge gaps remain, particularly for less-studied systems such as SPS with planted trees or shrubs. The predominance of studies on SPS with native trees (74.5%) reflects the extensive adoption of these systems, especially in Mediterranean countries such as Spain and Portugal, where *dehesa* and *montado* landscapes dominated by native oak species (*Quercus ilex* and *Q. suber*) provide a long-established model for integrated grazing and tree cover. These systems are culturally and economically significant and are characterised by low-intensity grazing regimes that are known to sustain high levels of biodiversity (Rodríguez-Rojo et al., 2022). SPS with native trees are usually extensive, mainly adding cattle into existing natural habitats to capture the benefits of trees and understorey vegetation for grazing with little additional inputs or management, whereas SPS with planted trees and SPS with shrubs are generally intensive, with a focus on profits through the joint productivity of livestock and timber or biomass (Peri et al., 2016; Jose and Dollinger, 2019; Smith et al., 2022). The limited number of studies on SPS with planted trees and SPS with shrubs also likely reflects the more restricted implementation of these systems, which require planned tree or shrub establishment (e.g., alley planting) or active stand management (e.g., thinning of plantations) to balance timber and livestock production (Poudel et al., 2022; Munaro et al., 2023). In addition, biodiversity studies often require extensive experimental areas to analyse the large home ranges of certain species and to minimise edge effects, whereas SPS with planted trees are usually established at small plot scales (Lopes et al., 2020; Poudel et al., 2022). Hence, larger long-term trials of SPS are required, and more research on biodiversity in these systems is needed to provide a comprehensive understanding of their biodiversity benefits.

The disparity in research effort across taxonomic groups highlights a critical gap in understanding the ecological value of SPS. Plants (42.9%) and invertebrates (27.8%) were well-studied, likely because these taxa are comparatively easier to sample and quantify using standardised, low-cost methods such as quadrat sampling, pitfall traps, and sweep netting. In contrast, birds, mammals, reptiles, amphibians, and microbial communities remain poorly studied because these groups require specialised survey techniques (e.g., acoustic monitoring, camera trapping, DNA, and sequencing) that are more resource-intensive and demanding in terms of technical expertise. Additionally, vertebrate studies also often require larger spatial scales to reduce edge effects, longer-term temporal monitoring, and compliance with animal ethics, which can restrict research interests. The current evidence likely underestimates the biodiversity values of SPS and requires further research on vertebrates and microbes.

### 4.2. Effect of SPS on biodiversity

In our meta-analyses, SPS exhibited a significantly positive effect on biodiversity compared to open pastures. This is because the integration of trees into livestock production systems enhances habitat complexity, resource availability, and ecological resilience compared to open grazing systems (McAdam et al., 2007; Auad et al., 2015; Xu et al., 2017; Bagella et al., 2020; Giraldo et al., 2024). The presence of trees on grasslands attracted more bird species (even at early stages of establishment) and epigeal invertebrates, which are food sources for birds (McAdam et al., 2007), whereas higher plant diversity in SPS was the key contributor to higher bird diversity in these systems (Giraldo et al., 2024). Moreover, the integration and interaction of multiple layers within SPS can enhance environmental conditions, thereby promoting the biodiversity of specific taxonomic groups, particularly ground invertebrates (Auad et al., 2015; Alonso et al., 2019; Gómez-Cifuentes et al., 2019; Vazquez et al., 2020). For instance, planting mixed tree species on pastures of signal grass (*Urochloa decumbens*) supported Hymenoptera communities (Auad et al., 2015), whereas integrating pasture species with native trees diversified vegetation structure, improved microclimate, which enhanced the diversity of dung beetles (Alonso et al., 2019). This was also reported by Gómez-Cifuentes et al. (2019) in SPS with loblolly pine (*Pinus taeda*), which created better microclimate and soil conditions to attract more dung beetle species. For instance, the use of a mix of legume and grass species in SPS improved soil quality and resulted in a higher richness of soil macrofauna (Vazquez et al., 2020). Importantly, SPS can also function as ecological corridors, facilitating landscape connectivity between open pastures and forest habitats. This connectivity plays a crucial role in facilitating the dispersal of species across fragmented landscapes (Mastrangelo and Gavin, 2012; McDermott et al., 2015).

Both SPS with native and planted trees significantly enhanced biodiversity relative to open pastures. SPS with native trees showed a greater positive effect size than SPS with planted trees. This is likely due to significant differences in the establishment and management practices of these two systems. SPS with native trees are typically established within existing natural habitats, maintaining much of the original structural complexity, microhabitat diversity, and mix of plant ages, resulting in stronger conservation outcomes (Gómez-Cifuentes et al., 2019; Aparicio-Lechuga et al., 2022). In contrast, SPS with planted trees usually involve site preparation, planting operations, and initial management interventions that can temporarily disturb soil, vegetation, and faunal communities, potentially affecting biodiversity gains in the early years following establishment (McAdam et al., 2007; Six et al., 2014). This finding highlights the importance of considering SPS design and establishment, particularly for SPS with planted trees, to balance between production and biodiversity conservation.

Compared to ungrazed native forests, SPS with native trees exhibited a significantly negative effect on biodiversity. This finding reinforces the ecological importance of native forests in supporting high levels of biodiversity (Gibson et al., 2011), while also highlighting the challenges of converting unmanaged native forests to SPS in terms of biodiversity conservation (McDermott et al., 2015). This may be partially explained by higher tree cover and vegetation complexity in ungrazed native forests, which favour various groups, particularly forest birds (Mastrangelo and Gavin, 2012; McDermott and Rodewald, 2014). Additionally, negative impacts of extensive grazing, including understory degradation, soil compaction, altered microclimate, and reduced regeneration capacity, are likely key drivers of biodiversity loss in SPS relative to ungrazed forest habitats. For instance, livestock grazing reduced ground vegetation biomass and plant richness (Lindgren and Sullivan, 2012; Lempesi et al., 2017). Such reductions can negatively impact other taxa; for example, ground invertebrates (Montoya-Molina et al., 2016; Kinneen et al., 2023) and grassland birds (Giraldo et al., 2024). However, the development of SPS in open native woodlands with suitable management practices (e.g, rotational grazing) can approximate certain ecological functions of ungrazed woodlands to benefit specific taxonomic groups (Alonso et al., 2019; Gómez-Cifuentes et al., 2019; Duque-Vélez et al., 2022; López-Ramírez et al., 2023). For example, the vegetation complexity of SPS created favourable microclimatic conditions, along with the presence of livestock, which supported the diversity of dung beetles (Alonso et al., 2019; Gómez-Cifuentes et al., 2019).

The comparative biodiversity effects of SPS with planted trees and ungrazed plantations may differ from the patterns observed between SPS with native trees and ungrazed native forests; however, the scarcity of studies on this SPS type and the limited availability of comparisons with planted forests precluded a robust meta-analysis of their effect on biodiversity. This once again underscores the need for additional biodiversity studies on SPS with planted trees in comparison with ungrazed plantations.

At the taxa level, SPS with native trees supported higher invertebrate biodiversity than open pastures. However, these two contrasting systems exhibited similar invertebrate abundance. This enhancement likely reflects the strong sensitivity of invertebrate communities to improvements in vegetation structure, soil, and microclimatic stability that typically arise when trees are incorporated into open grazing landscapes (Alonso et al., 2019; Vazquez et al., 2020). The integration of pasture and tree species can support diverse and even invertebrate communities by providing suitable habitats in different strata such as tree canopy, understory vegetation, ground litter, and soil (Alonso et al., 2019; Gaytán et al., 2021). In contrast, open pastures facilitate the dominance of a few invertebrate assemblages, particularly grassland-associated species (Veríssimo et al., 2021; Kinneen et al., 2023). However, when compared with native forests, SPS with native trees exhibited lower levels of invertebrate and plant biodiversity. These differences again underscore the superior ecological capacity of intact forests to support complex, specialised communities that cannot be fully maintained within grazing systems. It is important to note that the dominance of within-publication variation indicated that responses of these groups were likely influenced by different assessed metrics, site conditions, and management practices among SPS with native trees and their references within individual publications. Interestingly, bird biodiversity exhibited no significant difference between SPS with native trees and native forests. This indicates the ecological importance of native trees in grazing systems and the connectivity between these two habitats in supporting forest bird communities (Mastrangelo and Gavin, 2012; McDermott et al., 2015; Edo et al., 2024). For example, Mastrangelo and Gavin (2012) reported that SPS incorporating mixed native tree species attracted approximately 90% of forest bird species present in nearby forest fragments in Argentina. Similarly, Edo et al. (2024) found that SPS with native holm oak species maintained a bird diversity comparable to that of adjacent forests in Spain. Bird responses in SPS with native trees were primarily driven by differences among publications, suggesting potential landscape factors such as tree canopy cover, patch size, habitat connectivity, and presence of nearby native forests across the studied regions might influence bird communities in these systems.

Overall, the effect of SPS on biodiversity compared to their references depends on system types and taxonomic groups. SPS with native and planted trees enhanced biodiversity compared to open pastures, but the biodiversity level of SPS with native trees remained lower than that of ungrazed native forests. These findings have important implications for the development of tree-based grazing systems that aim to reconcile production with biodiversity conservation goals. Transitioning from open grazing to silvopastoral systems offers a promising pathway to enhance biodiversity. However, this transition might require potential trade-offs between production goals and ecological outcomes. Planting design and the application of suitable management practices should be considered to increase vegetation heterogeneity and structural complexity, thereby enhancing biodiversity. This study also suggests that the adoption of SPS with native trees provides a complementary approach to biodiversity conservation, rather than a direct substitute for native forests. To maximise the biodiversity benefits of these systems, management practices should aim to preserve soil quality and vegetation structures comparable to those in native forests. Especially, situating SPS adjacent to forest habitats or retaining surrounding forest remnants can support biodiversity conservation in grazing landscapes.

However, several limitations should be considered when interpreting the findings of this study. First, the literature search may not have captured all relevant research, particularly studies published in non-English languages, potentially limiting global representation. Second, restricting the dataset to studies that provided comparable quantitative information (sample size, mean, and standard deviation or error) led to the exclusion of extensive studies from the meta-analysis that examined species composition or reported only total richness or abundance without mean values. To ensure the robustness of meta-analysis, effect size calculations were limited to data subsets with more than 10 publications and 30 comparisons, even though no minimum threshold is required. Consequently, several relevant effect sizes (e.g., biodiversity of SPS with planted trees compared to native and planted forests or bird biodiversity of SPS with native trees relative to open pastures) were not analysed, and the results must therefore be interpreted in the absence of their effects. Furthermore, the effect of potential cofounding factors such as landscape context, tree density or canopy cover, system age, habitat connectivity, and management practices across SPS could not be addressed because selected publications did not adequately report these features.

## 5. Conclusions

Further research on biodiversity in SPS is needed, particularly in systems established with planted trees or shrubs in underrepresented regions. Moreover, future studies should expand beyond plants and invertebrates to examine the effect of SPS on vertebrates and microbes. This broader scope is essential to fully assess the biodiversity potential of SPS across all system types and taxonomic groups.

The effect of SPS on biodiversity compared to open pastures and ungrazed forests varied with system types and taxonomic groups. SPS increased biodiversity by 28.4% relative to open pastures. Both SPS with native and planted trees supported 36.3% and 20.9% greater biodiversity than open pastures, respectively. However, SPS with native trees had 18.1% lower biodiversity relative to ungrazed native forests. At the taxa level, native tree-based SPS exhibited similar biodiversity of birds, but lower levels of plants and invertebrates relative to native forests. In contrast, these native systems enhanced invertebrate communities compared to open pastures. These findings suggest that transitioning from open grazing to SPS represents a promising strategy to enhance biodiversity, and the development of SPS with native trees provides a complementary approach to biodiversity conservation, rather than a direct substitute for native forests.

## CRediT authorship contribution statement

**David J. Lee:** Writing – review & editing, Supervision, Conceptualization. **Tien Chinh Nguyen:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Nahuel A. Pachas:** Writing – review & editing, Project administration. **Teresa J. Eyre:** Writing – review & editing. **Helen F. Nahrung:** Writing – review & editing, Methodology, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

The manuscript was written and edited by all authors. ChatGPT (OpenAI) was used to improve the readability to ensure the manuscript is free of grammar and spelling errors. This tool was also used to generate Fig. 2, based on data summarised from selected publications. After using this tool, the authors carefully reviewed and edited the content and take full responsibility for the content of this publication.

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## Declaration of Competing Interest

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

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## Appendices.

**Table. A.1**
Number of data-extracted publications (N) and comparisons (K) according to silvopastoral system (SPS) types, taxonomic groups, biodiversity metrics, and comparisons

| Category | N | Percentage (%) | K | Percentage (%) |
|---|---|---|---|---|
| **SPS type** | | | | |
| SPS_n | 53 | 67.1 | 532 | 72.9 |
| SPS_p | 22 | 27.8 | 162 | 22.2 |
| SPS_s | 4 | 5.1 | 36 | 4.9 |
| **Total** | **79** | **100** | **730** | **100** |
| **Taxonomic group** | | | | |
| Invertebrate | 35 | 42.2 | 286 | 39.2 |
| Bird | 13 | 15.7 | 257 | 35.2 |
| Plant | 25 | 30.1 | 127 | 17.4 |
| Microbe | 6 | 7.2 | 45 | 6.2 |
| Mammal | 3 | 3.6 | 13 | 1.8 |
| Reptile | 1 | 1.2 | 2 | 0.3 |
| **Total** | **83** | **100** | **730** | **100** |
| **Biodiversity metric** | | | | |
| Richness | 55 | 39.0 | 280 | 38.4 |
| Abundance | 42 | 29.8 | 269 | 36.8 |
| Diversity | 32 | 22.7 | 141 | 19.3 |
| Evenness | 12 | 8.5 | 40 | 5.5 |
| **Total** | **141** | **100** | **730** | **100** |
| **Comparison type** | | | | |
| SPS_n vs NF | 45 | 42.5 | 383 | 52.5 |
| SPS_n vs OP | 26 | 24.5 | 146 | 20.0 |
| SPS_p vs OP | 18 | 17.0 | 105 | 14.4 |
| SPS_p vs PF | 5 | 4.7 | 33 | 4.5 |
| SPS_s vs OP | 4 | 3.8 | 28 | 3.8 |
| SPS_p vs NF | 4 | 3.8 | 24 | 3.3 |
| SPS_s vs NF | 2 | 1.9 | 5 | 0.7 |
| SPS_s vs PF | 1 | 0.9 | 3 | 0.4 |
| SPS_n vs PF | 1 | 0.9 | 3 | 0.4 |
| **Total** | **106** | **100** | **730** | **100** |

*Note:* SPS_n = SPS with native trees, SPS_p = SPS with planted trees, SPS_s = SPS with shrubs, and OP = open pastures, NF = native forests, PF = planted forests.

**Table A.2**
Heterogeneity between publications ($\sigma^2$Between) and within publications ($\sigma^2$Within). Percentages indicate the proportion of total heterogeneity attributable to each level

| Subset | $\sigma^2$Between | $\sigma^2$Within | $\sigma^2$Total | Between (%) | Within (%) |
|---|---|---|---|---|---|
| Biodiversity_SPS vs OP | 0.23 | 0.19 | 0.42 | 55 | 45 |
| Biodiversity_SPS_n vs OP | 0.37 | 0.22 | 0.59 | 63 | 37 |
| Biodiversity_SPS_n vs NF | 0.12 | 0.11 | 0.23 | 51 | 49 |
| Biodiversity_SPS_p vs OP | 0.06 | 0.19 | 0.25 | 25 | 75 |
| Plant_SPS_n vs NF | 0.04 | 0.10 | 0.14 | 26 | 74 |
| Bird_SPS_n vs NF | 0.11 | 0.04 | 0.15 | 74 | 26 |
| Bird richness_SPS_n vs NF | 0.08 | 0.03 | 0.12 | 71 | 29 |
| Invertebrate_SPS_n vs OP | 0.29 | 0.38 | 0.67 | 44 | 57 |
| Invertebrate_SPS_n vs NF | 0.16 | 0.30 | 0.45 | 35 | 65 |
| Invertebrate abundance_SPS_n vs OP | 0.38 | 0.95 | 1.33 | 28 | 72 |
| Invertebrate abundance_SPS_n vs NF | 0.06 | 0.81 | 0.88 | 7 | 93 |

Note: SPS = Silvopastoral systems; SPS_n = SPS with native trees, SPS_p = SPS with planted trees, OP = open pastures, and NF = native forests
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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110645.

## Data availability

Data will be made available on request.

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