Biological Conservation 307 (2025) 111182

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Review

Single- vs mixed-species plantations: A systematic review on the effects on biodiversity

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ARTICLE INFO

Keywords:
Mixed-species plantations
Biodiversity
Forest-related taxa
Meta-analysis
Systematic review
Restoration
Afforestation

ABSTRACT

Despite increasing evidence suggesting mixed-species plantations promote biodiversity, a comprehensive quantitative analysis of this knowledge is lacking. We systematically reviewed 71 studies to evaluate the effects of mixed versus pure tree plantations on biodiversity. Using descriptive statistics and meta-analyses, we explored: a) the effects of mixed plantations on forest-related biodiversity; b) variations in these effects with climate, stand age, and with the richness, relative abundance, and functional diversity of the planted species; and c) differences in responses across taxonomic and functional groups. Our meta-analyses revealed a significant positive effect of mixed-species plantations on taxonomic diversity. However, most observations (64%) reported no significant effects. Positive effects are more frequent in mixtures with more than two species (49%), compared to two-species mixtures (29%), and were strongest in tropical climates (78%), followed by temperate (26%) and continental climates (14%). Among taxonomic and functional groups, positive mixing effects are most frequent for birds (75%), followed by litter microbiota (47%), understory plants (40%), and above-ground arthropods (29%), while soil-dwelling micro-organisms (22%) and soil mesofauna (4%) appear less sensitive. Mixing conifers and broadleaves does not enhance biodiversity benefits, suggesting higher functional diversity may be better achieved by targeting specific species and traits. The limited effects of mixing observed in some cases may reflect the young age of plantations studied (11±9.4 years on average), which may limit the time for biodiversity to respond. The variability in biodiversity outcomes highlights the need for tailored mixing strategies and further research across broader plantation ages, settings, and underrepresented taxonomic groups to optimize biodiversity benefits in mixed-species plantations.

1. Introduction

Owing to a growing demand for a larger variety of goods and services from forests, and to an increased vulnerability of forest ecosystems to climatic extremes, the last decades have witnessed an increasing interest in diversifying forest structure and composition (Scherer-Lorenzen et al., 2005; Allen et al., 2010; Puettmann et al., 2012; Seidl et al., 2017; Messier et al., 2022). Tree species diversity, in particular, is expected to enhance ecosystem functioning and stability in the provision of goods and services (Gamfeldt et al., 2013; Bauhus et al., 2017a). This idea is supported by a growing body of evidence, including systematic reviews of scientific literature (Zhang et al., 2012; Castagneyrol et al., 2014; Liang et al., 2016). However, much of this knowledge is derived from studies with a focus on ecosystem productivity as a response variable, which is often used as a proxy for ecosystem functioning in general. Other ecosystem functions and properties, such as the diversity of forest-related taxa, have received less attention, likely due to the complexity of its assessment given the variety of different life forms involved, as well as their spatial and temporal variability (Loreau, 2000; Bauhus et al., 2017b).

As foundational species, trees provide habitat for a wide range of other species. The relationship between tree species diversity and forest-related biodiversity, however, is complex and often shaped by site conditions and the ecological interactions among species (Tedersoo

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https://doi.org/10.1016/j.biocon.2025.111182
Received 13 December 2024; Received in revised form 14 April 2025; Accepted 19 April 2025
Available online 24 April 2025

et al., 2016). The overall notion of higher ecosystem functioning and stability through higher species diversity is mainly based on the complementarity, insurance, and selection hypotheses. According to the complementarity hypothesis, a higher number of species can enhance ecosystem processes through positive interactions among species, either through competitive reduction or through facilitation among species (Tilman et al., 1997; Loreau, 2000; Hooper et al., 2005). According to the insurance hypothesis, in a species-rich ecosystem the loss of one species may be compensated by the presence of another species with a similar or redundant role, thereby providing for stability in the provision of the related function (Loreau, 2000; Hooper et al., 2005; Bauhus et al., 2017b). Finally, the selection hypothesis states that certain species might have a disproportionally large effect on ecosystem properties or functions. Consequently, a higher species richness would imply a higher likelihood that those species are included in the community (Huston, 1997; Loreau, 2000; Hooper et al., 2005; Bauhus et al., 2017b).

Tree species that are complementary in the use of resources may use the available growing space more efficiently, thereby increasing their chances to provide habitat for different life forms. Furthermore, they may also be complementary in the resources they provide for forest-related taxa, which is particularly the case when they exhibit different structural and functional traits (Cadotte et al., 2011; Cavard et al., 2011; Ampoorter et al., 2020). Forest stands with a higher trait diversity are likely to sustain a wider range of environmental conditions, resources, and microhabitats, thereby supporting a higher diversity of forest-related taxa (Ampoorter et al., 2020; Juchheim et al., 2020). This is often reflected in the presence of species-specific interactions between tree species and their related biodiversity, highlighting the importance of species identity in maintaining overall biodiversity (De Groote et al., 2017).

While studies addressing the effects of tree diversity on overall biodiversity are becoming increasingly abundant, they vary widely in their methodological approach and in the taxonomic groups on which they focus to evaluate biodiversity (e.g., Barsoum et al., 2014; Staab et al., 2015; Ji et al., 2020; Beason et al., 2023). In addition, the effects of tree diversity on ecosystem functioning are known to vary significantly in space and time (Paquette and Messier, 2011; Forrester and Bauhus, 2016). Despite the efforts by Cavard et al. (2011) and Ampoorter et al. (2020) to comprehensively describe the effects of tree diversity on the diversity of forest-related taxa, we still lack a quantitative systematic approach to synthesize evidence on these effects, particularly addressing their variation across different environmental and stand conditions. In this context, planted tree diversity experiments offer a valuable framework for evaluating general trends in the effects of tree diversity on biodiversity, as they control for key confounding factors at local and regional scale (Verheyen et al., 2016; Bauhus et al., 2017b). Moreover, the intended large-scale expansion of forest cover driven by global commitments to restoration and climate change mitigation and adaptation, is expected to strongly rely on planting, since this method can ensure rapid establishment of desired species, particularly when natural regeneration is insufficient (Holl and Aide, 2011; Simonsen, 2013; VanBijsterveldt et al., 2022). While this massive drive for new tree-plantation has been proposed as an efficient method to restore landscapes and increase sequestration of atmospheric CO_2 as nature based solutions (Griscom et al., 2017), single-species afforestation remains a subject of debate (Seddon et al., 2020). As a consequence, there is growing advocacy for mixed-species plantations to achieve this expansion, as they are expected to provide broader ecological benefits (Messier et al., 2022). Thus, evidence-based guidelines for establishing diverse planted forests to ensure that they provide the anticipated benefits are increasingly needed.

In this study, we conducted a systematic review to examine the effects of mixed vs pure plantations on tree- or forest-related biodiversity, using indices of taxonomic diversity as a proxy for biodiversity as a whole. Our aim was to identify both global and regional patterns in the response of biodiversity to mixed plantations, considering overall taxonomic biodiversity as well as specific taxonomic groups. In addition, we examined variations across different regions, climates, and ecological and management conditions. Specifically, we addressed the following questions: a) What are the effects of mixed-species plantations on the biodiversity of forest-related taxa?; b) how do these effects vary with climate, stand age, and with the richness, relative abundance, and functional diversity of planted species?; c) how do these effects vary for different taxa?

With the purpose of maximizing both the representativeness and the accuracy of our analyses, we combined two different approaches to address these questions: a) an analysis based on the general trends informed by a larger number of studies; and b) meta-analyses based on specific quantitative variables provided by a smaller sample of studies. These analyses will provide insights into the underlying processes that drive the effects of mixed-species plantations on biodiversity, while summarizing the current knowledge base relevant for developing biodiversity-friendly forest restoration practices.

2. Methods

This study was conducted following the PRISMA guidelines for adequate reporting in systematic reviews (Page et al., 2021), and the extended guidelines of Synthesis Without Meta-Analysis (SWiM), to be used in systematic reviews when estimating effect sizes is either not possible or fully adequate (Campbell et al., 2020). Furthermore, since the literature search was conducted in June 2022, only studies published up to that date were included in the analysis.

2.1. Literature search

We organized the search on the basis of the main components of the review question (Table 1). Each of the column names represents a different component, and the terms within it, either a synonym or a concept related to it. Along the search string, the different components were linked with the Boolean operator "AND", whereas the different terms within each component category were linked with "OR".

Analogue searches were conducted in Web of Sciences (WOS), Wiley Online Library, and Ovid, on the 28th of June 2022, using the search fields described in Table 2 (see Table S1 for the corresponding search strings).

To assess the suitability of the search string, we compared the search outcomes against a sample of four pre-selected studies published up to 2021, when this study was formulated (Table S2). Specifically, we verified whether these studies, which were preliminarily selected as representative examples of relevant research, appeared in the search results of at least one search engine. If any were missing, we refined our search terms by incorporating overlooked synonyms of key research components or adding wildcards to capture alternative word endings.

2.2. Study selection

After removing duplicates, we screened the complete list of studies by reviewing title and abstract, and discarded those studies that did not

Table 1
Components of the research question and their corresponding synonyms or related terms. The wildcard or asterisk symbol (*) stands for alternative word endings.

Intervention	Comparison		Outcome
	Pure plantation	Mixed plantation	
Plantations	Pure	Mixed	Biodiversity
Planting	Mono*	Polyculture	Diversity
Reforest*	Single	Multiple	Shannon
Afforest*		Multi-spec*	Simpson
Restor*			Richness

Table 2
Search fields in which each of the string components were searched for in each database, and the number of records retrieved in each case.

Database	Search fields	Outcome (n° of studies)
Web of Science	"All fields"	684
Wiley Online Library	*"Abstract"*	1024
Ovid	*"Title"; "Abstract"; "Identifiers"*	280

address the research question or were not peer-reviewed articles from scientific journals, or for which no full-text version could be obtained either online or from the authors. Subsequently, we conducted a full-text assessment of the remaining studies to evaluate the following inclusion criteria: (1) the study was based on a field experiment (either manipulative or observational); (2) a relevant comparison was conducted, (i.e., pure even-aged tree plantations vs mixed-species even-aged tree plantations of same or similar age (<20% difference among them)); (3) a relevant outcome was provided (i.e., indicators of biodiversity such as richness and diversity of taxa); (4) means and standard deviations of the biodiversity indicators, or results of statistical tests were provided. Forests were considered plantations, if the canopy trees were planted or sown, meaning that plantations could also include naturally-regenerated understory trees. Additionally, planted forests were considered mixed if they included two or more species among the canopy trees. For studies requiring subscription to a specific journal to be accessed, we addressed the authors directly to request a digital copy.

2.3. Data extraction

As expected, different studies used different indicators and taxonomic or functional groups to quantify biodiversity. The output for each indicator reported in a single study for a given taxonomic or functional group was deemed as an individual observation. Several studies reported multiple indicators of biodiversity, and these were evaluated either on a single or on multiple taxonomic or functional groups. Thus, a single study could report multiple observations, and consequently, the total number of observations was larger than the number of studies included.

In addition to including multiple indicators of biodiversity and taxonomic or functional groups, studies often included not just one, but different types of monocultures composed of different tree species. Similarly, some studies included different mixed-plantation treatments, involving either different sets of tree species, or different relative abundances of the same set of species. In addition, in some studies the effects of mixing were evaluated in plantations at different experimental sites, at different tree ages, or at different soil depths, and separate results were provided for each of these specific cases. The results reported for each of these different possibilities and their combinations were treated as sub-observations.

Based on the data provided, each observation and sub-observation was classified as reporting a significant or a null effect, and significant effects ($p<0.05$) were classified as positive or negative.

For conducting meta-analyses of the effects of mixed plantations on biodiversity, we extracted the means and standard deviations, standard errors, or confidence intervals of the reported biodiversity indicators for both the pure and the mixed plantations under comparison, as well as the sample sizes involved, whenever this information was provided. When only available in graphical format, the means and standard deviations were extracted using WebPlotDigitizer (Rohatgi, 2022). When values of standard errors were provided, these were transformed into standard deviation by multiplying them by the square root of the sample size. Alternatively, when 95% confidence intervals were provided, these were transformed into standard deviation by dividing the length of the confidence interval (i.e., the absolute difference between the upper and lower limits) by 3.92, and multiplying the result by the square root of the sample size.

2.4. Data synthesis

To assess the effects of mixed-species plantations on biodiversity, we employed two complementary approaches: a trend analysis and meta-analyses. The trend analysis examined the frequency with which studies reported significant effects of mixed-species plantations on biodiversity and whether these effects were positive or negative. This approach required minimal data for inclusion, allowing for broader literature coverage. However, it did not account for effect sizes or differences in statistical power, which could introduce biases. To address these limitations, we conducted meta-analyses, which require studies to report means, standard deviations, and sample sizes. While this restricts the number of studies that can be included, it provides a more robust quantitative output by using these data to account for effect sizes and statistical power.

2.4.1. Data for trend analyses

We classified the reported biodiversity indicators into four main types: species richness, species diversity, functional diversity, and phylogenetic diversity. Similarly, due to the large number of reported taxonomic or functional groups and the similarities among them, we grouped them into corresponding categories (Table S3). We recorded the frequency of null, positive, and negative effects of mixed vs pure plantations overall, for each type of biodiversity indicator, and for each of the categories of taxonomic or functional groups (Page et al., 2021). To prevent biased results towards studies with sub-observations (i.e., with more than one output for a biodiversity indicator for a given taxonomic or functional group), the output for each sub-observation was weighted by the total number of sub-observations addressed in the corresponding study.

Additionally, to assess whether the occurrence of significant effects was influenced by study sample size, we calculated the point-biserial correlation coefficient between study sample sizes and the frequency of significant effects (whenever sample sizes were reported). This coefficient quantifies the strength and direction of the relationship between a binary variable (i.e., whether an effect was significant or not) and a continuous variable (i.e., study sample size). A positive correlation would suggest that larger studies tend to report more significant effects, potentially indicating sample size bias (Tate, 1954; Kornbrot, 2014).

We evaluated the influence of context-related factors (hereafter moderators) on the effects of mixed plantations, by comparing the overall frequency of null, positive, and negative effects of mixed-species plantations on measures of biodiversity reported by studies in different climate types (temperate; continental; tropical; dry), addressing plantations of different ages (<5 years; ≥5 and <20 years; >20 years), and involving mixed plantations with varying degrees of tree species richness (2 species; 3–5 species; >5 species), relative abundances (even vs uneven abundance of the component tree species), and functional diversity (i.e., including both conifers and broadleaves vs including only conifers or broadleaves) (Table 3). We considered the presence of both conifers and broadleaves in a mixed plantation as an indicator of a higher functional diversity. Species in a mixed plantation were considered unevenly abundant if their share differed by >10%.

Some moderator classes (e.g., specific climate types, age classes, levels of tree species richness, etc.) may have been biased towards plantations with a higher number of species, which eventually may result in a higher functional diversity. To prevent this bias, we explored the number of species involved in the mixed plantations across the different moderator classes. This bias was confirmed for the climate types. While 70% of mixed plantations in tropical regions included more than two species, only 13% and 14% of mixed plantations in temperate and continental regions did so. It was also the case for the functional diversity classes (i.e., mixing either broadleaves and conifers, or mixing only broadleaves or conifers). While 91% of the mixed plantations with both conifers and broadleaves included more than two species, only 45% of the plantations including only conifers or broadleaves did so

Table 3
Analyzed moderators of the effect of mixed- vs pure plantations.

Climate	Age class[1]	Types of mixed plantations used		
		N° of species[1]	Relative abundance of mixed species[1]	Types of species used[1]
1) Temperate 2) Continental 3) Tropical 4) Dry	1) <5 years 2) ≥5; <20 years 3) >20 years	1) 2 2) >2; ≤5 3) >5	1) Even 2) Uneven	1) Both conifers or broadleaves 2) Either conifers or broadleaves

[1] Moderators for which comparisons were possible both among and within single studies.

(Table S4). In these two cases, we controlled for the influence of the number of species mixed by selecting studies with only two-species mixtures. Accordingly, since all studies from dry regions (n=3) involved mixed plantations with >2 species, they were excluded from this analysis.

Meaningful comparisons among climate types and functional diversity classes for mixed plantations with a number of species higher than two were not possible due to the low number of studies.

2.4.2. Meta-analyses

We conducted multiple meta-analyses in R (version 4.4.1) (R Core Team, 2022) to evaluate the effect of tree species mixing. As an general input for these analyses, we calculated Hedges' d (Hedges and Olkin, 2014) for each study, using the reported means, standard deviations and sample sizes, employing the "Metafor" package (Viechtbauer, 2010). Since some studies included multiple observations, we aggregated the corresponding effect sizes into a single combined effect size per study using the "aggregate" function from this package. We assumed the multiple outcomes from the corresponding study to be independent from each other (Viechtbauer, 2010). For the meta-analyses, we used random effects models to estimate the mean effect sizes, in order to account for both the within-study variance (i.e. the sampling error) and the between-study variance of the effect size (Borenstein et al., 2021). We conducted an overall meta-analysis, including all studies grouped together, and specific meta-analyses for each of the main biodiversity indicators reported by at least five studies. In addition, we conducted separate meta-analyses for effect sizes grouped according to the moderator classes described above (Table 3) and the taxonomic/functional group categories for which biodiversity levels were reported, whenever the corresponding number of studies was equal to or greater than five. In these cases, however, we grouped the effect sizes by moderator class and taxonomic/functional group categories, respectively, before aggregating them by study, as opposed to for the overall meta-analysis. This enabled us to retain the information form sub-observations before grouping, allowing us to refine the scale of analysis by classifying not only whole studies according to moderator classes, but also specific sub-observations. As for the trend analyses (2.4.1), for the moderators climate type and functional diversity, we controlled for the influence of the number of species mixed by selecting studies with only two-species in mixed plantations.

3. Results

From the 7009 studies obtained from the different databases, 635 were discarded as duplicates. Of the remaining, 6175 were discarded after title and abstract screening. The remaining 199 studies were subjected to full-text reviewing. Following the inclusion criteria for this stage, 71 studies were finally considered relevant and were included in the review (Fig. S1; Table S5).

3.1. Overview of the evidence base

The studies finally included in this review span from 1997 to 2022. However, the majority was published after 2006. During this period, the number of studies published per year indicates an increasing trend in time (Fig. 1).

Most of the studies were conducted in Eastern and South-Eastern Asia (34%), Central and South America (28%), and Europe (23%), and only a few in Africa (7%), Oceania (6%), and North America (1%) (Fig. 2). More than half of the studies (54%) were conducted under a temperate climate type, and 31%, 11%, and 4% under tropical, continental, and dry climate types, respectively, according to the Köppen classification (Figs. 2 and 3).

Regarding the nature of the experiments, the age of plantations evaluated ranged between 1 and 100 years, with an average of 11±9.4 years. In most studies (70%), the mono-specific and the mixed plantations under comparison were of similar age. In these cases, observations were relatively evenly distributed among the pre-defined age classes (≤5 years; >5 and ≤20 years; >20 years), with a higher proportion of studies (41%) focusing on the early stages (Fig. 3). Most studies (82%) involved multiple pure plantations, each consisting of a different species. Similarly, 65% of the studies compared different varieties of mixed plantations, either by varying the number and identity of the species, or their relative abundance. Fifty-four percent of the studies included only two species in the mixed plantations, while the rest included two or more species, and 23% included more than five species (Fig. 3). From the studies informing the composition of the mixed plantations, 42% involved both conifer and broadleaved species, while the rest (58%) involved either conifers or broadleaves (Fig. 3). Additionally, 61% of the studies had an even distribution of species abundances in the mixed plantation (e.g., 50% of species A, and 50% of species B at the time of planting), whereas in 39% of them, the species in the mixed plantations had uneven abundances (e.g., 30% seedlings of species A, and 70% of species B).

3.2. Categories of taxonomic and/or functional groups

In the 71 studies included, responses of 27 different taxonomic and/or functional groups were reported. Based on their similarities, we grouped them into six main categories (Table S3). Soil micro-organisms (fungi, bacteria, and archaea) were the most frequently surveyed groups (41%), followed by understory plant species (28%), above-ground arthropods (14%), birds (9%), soil mesofauna (5%), and litter micro-organisms (4%). Apart from birds, no other vertebrate group was addressed (Fig. S2). In terms of the indicators provided, most of the observations reported species richness (48%) or diversity (as Shannon-Wiener, Simpson, Chao, or Fischer's alpha) (42%), while a minor part of the observations reported measures of phylogenetic diversity (6%) and functional diversity (4%).

3.3. Effects of mixed-species plantations on biodiversity

In total, 137 observations were obtained. According to the trend analyses, 33% of the observations reported significant positive effects of mixed-species plantations on biodiversity, 3% reported significant negative effects, and 64% of the observations reported no significant effects. In terms of the type of indices reported, only species diversity indices (Shannon-Wiener, Simpson, Chao, or Fischer's alpha) and species richness had >10 observations. Species diversity indices show a higher sensitivity to mixing than species richness, with 38% vs 25%

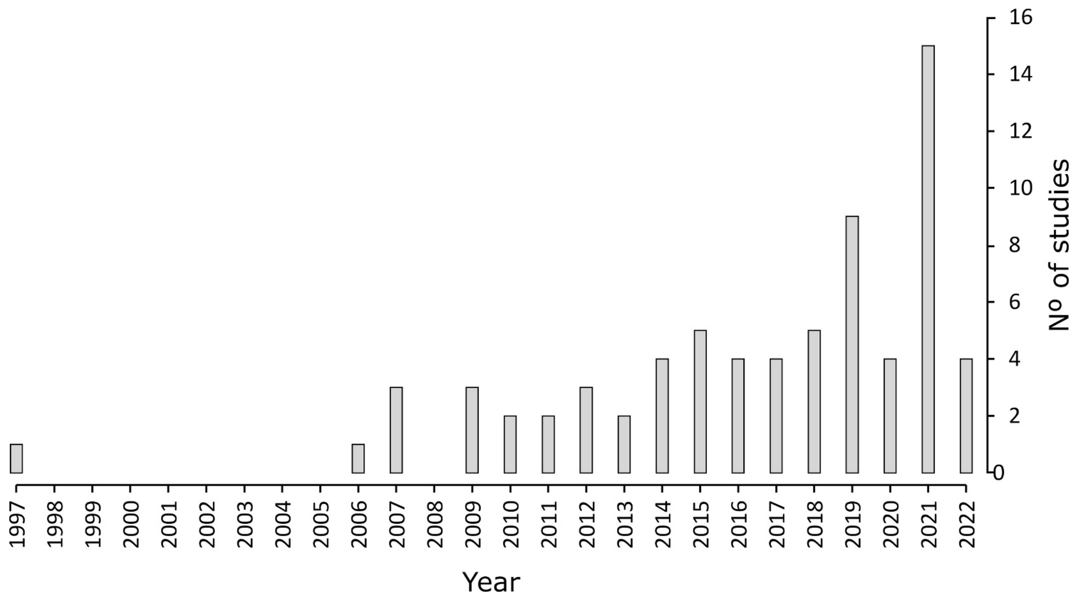

Fig. 1. Number of studies included in our analyses per publication year. Since the literature search took place in June 2022, the actual number of studies published in that year was likely higher than is depicted here.

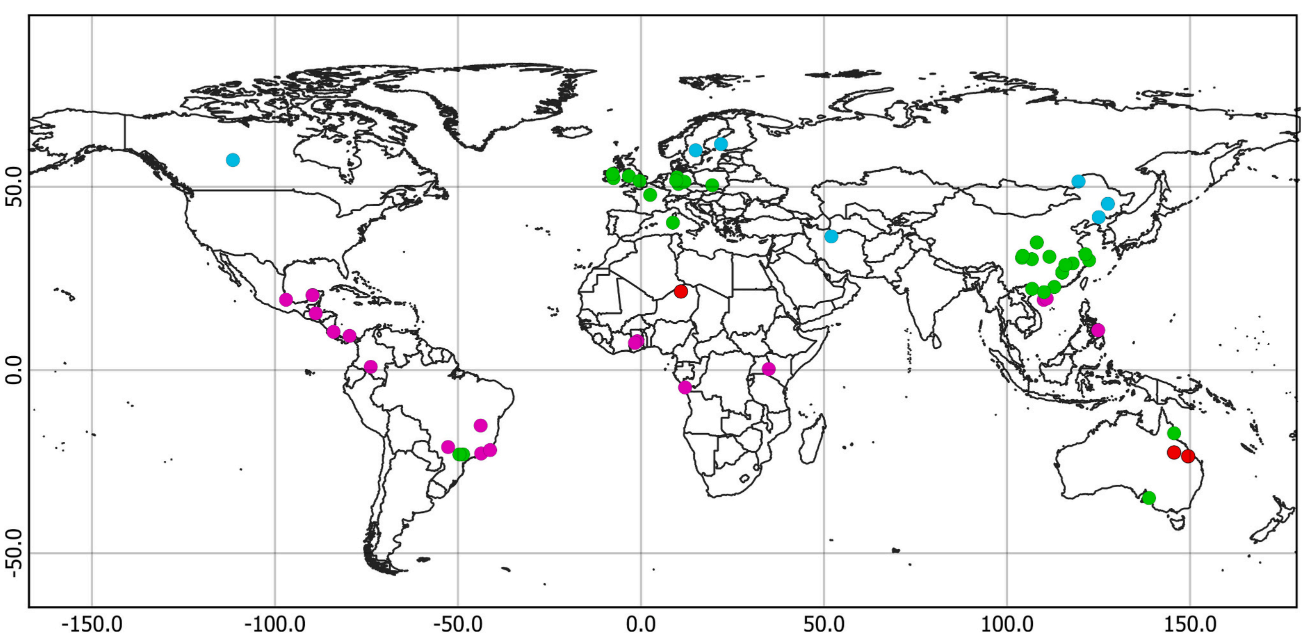

Fig. 2. Location of the studies included. Light blue, red, green, and purple dots represent studies conducted in continental, dry, temperate, and tropical regions, respectively, according to the Köppen climate classification (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

significant positive effects. Significant negative effects, however, were similarly infrequent among both types of indices (3%). According to the few observations reporting effects on phylogenetic and functional diversity, these indicators are the most sensitive to mixing, with 58% and 39% significant positive effects, respectively, and no negative effects (Fig. 4).

In line with the overall trend, when comparing outputs based on the different moderator classes, the significant effects were mostly positive, while negative effects were either absent or negligible, with significant negative effects ranging from 0 to only 7% of the total number of observations in each case (Fig. 5). Studies conducted under tropical climatic conditions show a considerably higher proportion of significant effects on biodiversity with 75% of observations showing significant effects, when compared to those in temperate and continental climates, with 26% and 14%, respectively. Yet, for the tropical climate type there were only eight observations. The proportion of significant effects shows a slightly decreasing trend with increasing plantation age, with 41% in plantations ≤5 years old, 32% in plantations >5 and ≤ 20 years old, and 25% in plantations >20 years old.

The frequency of significant effects on biodiversity is higher in mixed plantations with more than two species than in those with only two species. For two-species mixed plantations, the effect of mixing is significant in 29% of the cases. In contrast, for mixed plantations with three to five species, and with >5 species, the proportion of significant positive effects is 51% and 49%, respectively. Furthermore, for mixed plantations with >5 species, the effects of mixing are exclusively

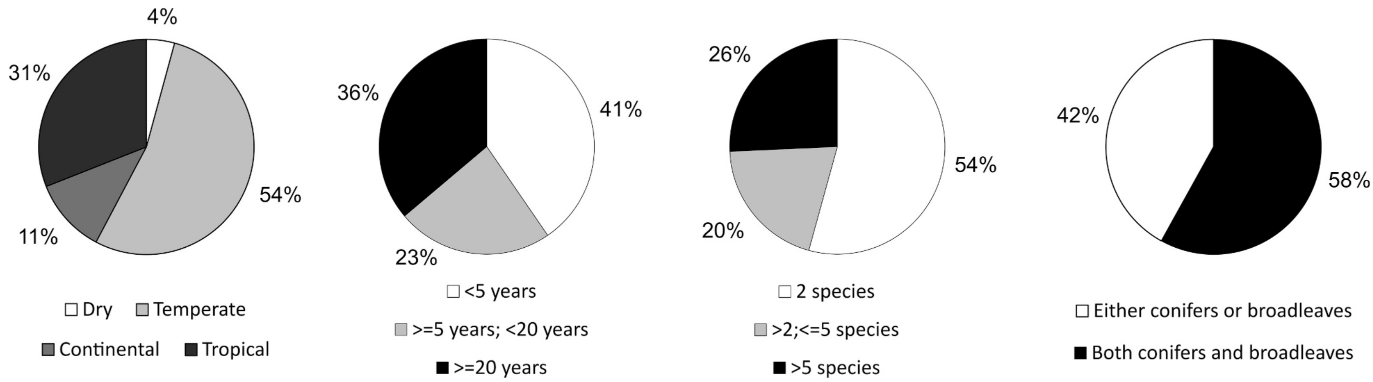

Fig. 3. Distribution of the observations based on a) climate types; b) age classes; c) tree species richness of the mixed plantations; and d) species types present in the mixed plantations.

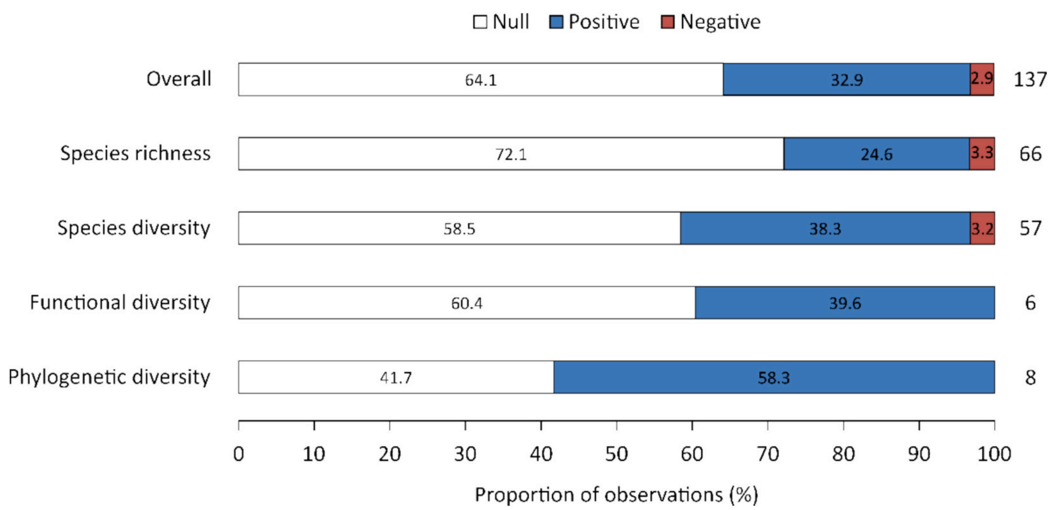

Fig. 4. Frequency of observations indicating positive, negative, and null effects of mixed-species plantations on biodiversity, for the different types of indices reported. Values within the bars indicate the frequency (%) of each effect type. Values on the right indicate the number of observations in each case. The percentages shown resulted from calculations based on the output either of whole observations or of sub-observations, depending on the nature of the studies.

positive, whereas in mixtures with fewer tree species, a small proportion of negative effects (3–5%) is observed.

In contrast, the influence of the relative abundance of tree species in the mixture is limited. Plantations with even abundances of planted species have a slightly higher frequency of significant effects compared to those with uneven abundances (36% vs 31%). Finally, mixing seems considerably more effective when using either conifers or broadleaves instead of combining conifers and broadleaves in the same mixture, with 36% significant positive effects in the first case, and 18% in the latter.

In terms of the main taxonomic/functional groups (Table S3), all groups had >10 observations except for litter microbiota (n=5) and soil mesofauna (n=6). The frequency of significant effects shows considerable variation among the groups. The highest proportion of significant effects was registered for birds, with 75%, and the lowest, for soil mesofauna, with only 4%, all of which were positive. For litter microbiota, understory plant species, and above-ground arthropods, the proportions of significant effects were similar, with 47%, 40%, and 38%, respectively. Yet, for above-ground arthropods the significant effects were partly negative, with 10% significant negative effects, while for litter microbiota and understory plants, all significant effects were positive. Soil microbiota showed a relatively lower sensitivity to mixing, with 26% significant effects, with 22% positive effects, and 4% negative effects (Fig. 6).

The point-biserial correlation between the sample size of the studies and the frequency of significant results was 0.26 (p<0.01), indicating a moderate positive association between the variables.

3.4. Meta-analyses

Of the 71 included studies, 47 provided the necessary information for inclusion in meta-analyses (Table S5). Of these, 40 studies provided suitable data for analyzing the effects of mixed plantations on species richness, and 30 for the effects on indices of species diversity (Shannon-Wiener, Simpson, Chao, or Fischer's alpha). Neither phylogenetic nor fuFnctional diversity had at least five observations, and thus, no specific meta-analyses were conducted for these indicators. According to the overall meta-analysis, in which all the observations were grouped together, mixed-species plantations have a significant positive effect on biodiversity. The specific meta-analyses for both species richness and species diversity indices showed consistent results, indicating significant positive effects in each case, with a higher effect size estimate for species diversity indices (Fig. 7).

When dividing observations among moderators, the corresponding meta-analyses were consistent with the overall results, showing positive effects in each case. However, according to these results, the positive effects of mixed plantations were only significant for younger stands (0 to 5 years), when mixing more than two species, and when mixing species in even proportions (Fig. 7). The influence of climate could not be evaluated due to the lack of observations for the specific climate types.

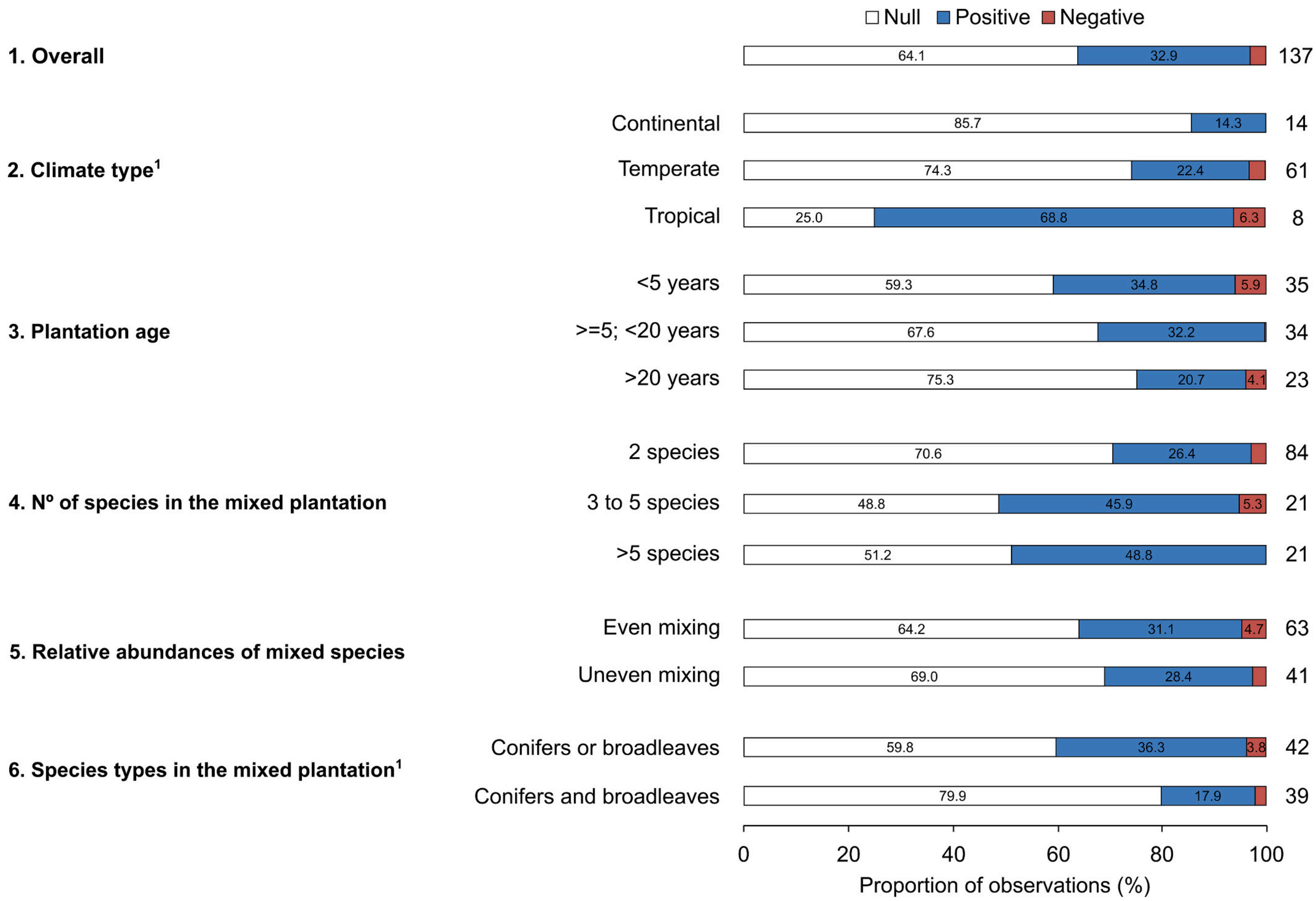

Fig. 5. Frequency of observations indicating positive, negative, and null effects of mixed-species plantations on biodiversity. Values on the right indicate the number of observations in each case. The percentages shown resulted from calculations based on the output either of whole observations or of sub-observations, depending on the nature of the studies. [1]For these moderators, the analysis was restricted to studies with two-species mixtures. This was due to the uneven distribution of the number of species mixed across the corresponding classes: mixtures in continental and temperate climates were mostly two-species mixtures, whereas mixtures in tropical climates were in most cases >2-species mixtures. Similarly, mixtures involving both conifers and broadleaves were in most cases two-species mixtures, whereas mixtures involving only conifers or only broadleaves were split more evenly between two-species and >2-species mixtures (see Table S4).

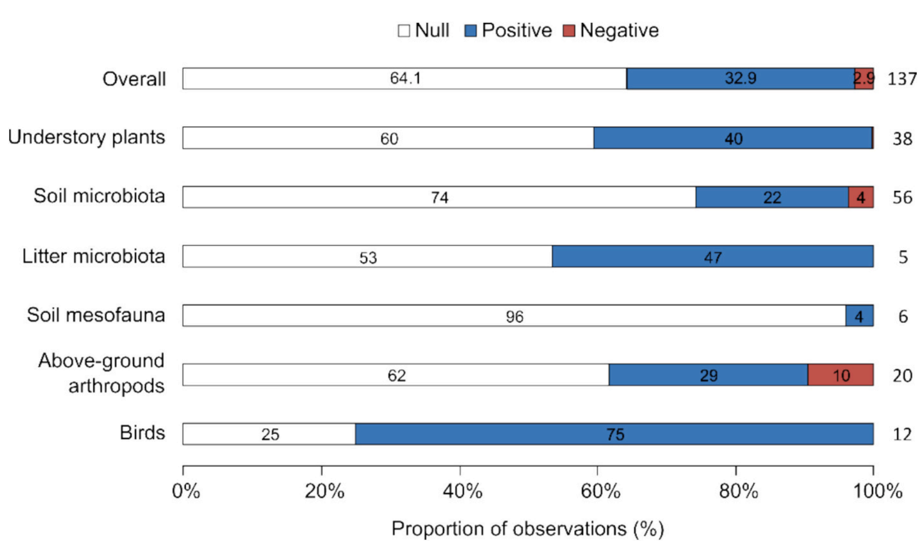

Fig. 6. Frequency of observations indicating positive, negative, and null effects of mixed-species plantations on biodiversity, for each of the taxonomic/functional groups. Values within the bars indicate the frequency (%) of each effect type. Values on the right indicate the number of observations in each case. The percentages shown resulted from calculations based on the output either of whole observations or of sub-observations, depending on the nature of the studies.

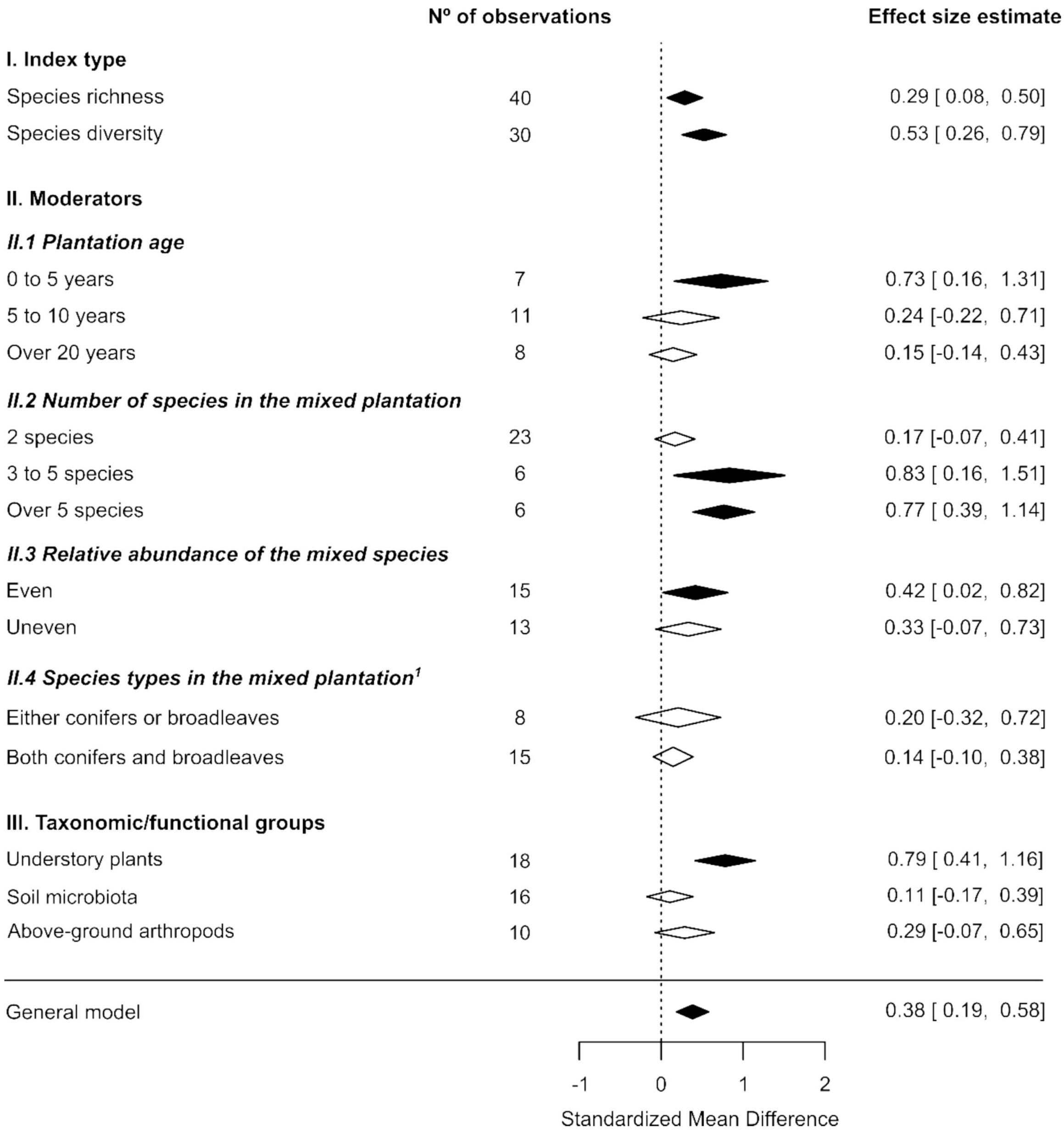

Fig. 7. Forest plot of the meta-analyses on the effects of mixed-planting on biodiversity, for the different indices, moderator classes, and taxonomic or functional groups. Only categories or classes with ≥5 observations were included. The centroids of the polygons indicate the point estimate of the combined standardized mean difference between pure and mixed plantations for each group of studies or observations, while their outer edges indicate the 95% confidence interval limits. Polygons not intersecting the null effect axis (represented by the vertical line) indicate a significant difference between pure and mixed plantations (Viechtbauer, 2010). For this moderator, the analysis was restricted to studies with two-species mixtures. This was due to the uneven distribution of the number of species mixed across the corresponding classes: mixtures involving both conifers and broadleaves were in most cases two-species mixtures, whereas mixtures involving only conifers or only broadleaves were split more evenly between two-species and >2-species mixtures (see Table S4).

Regarding taxonomic or functional groups, only understory plants, soil microbiota, and above-ground arthropods had enough observations for conducting meta-analyses (≥5), with 18, 16, and 10 observations in each case, while litter microbiota, soil mesofauna, and birds did not have a sufficient number of observations. All the surveyed groups suggest a positive effect of mixed plantations on biodiversity. However, this trend was significant only for understory plants (Fig. 7).

4. Discussion

4.1. Overall patterns

Our systematic review of scientific studies on the effects of mixed- vs pure tree plantations on forest-related biodiversity reveals an overall positive effect of mixed plantations on biodiversity. The trend analyses indicated that whenever significant, the effects of mixing are almost exclusively positive, with only a minor proportion of negative effects. Similarly, the overall meta-analysis indicates a significant positive effect of mixing, which is consistent with the trends shown by the specific meta-analyses for the different indices, moderator classes, and taxonomic/functional groups. Yet, according to the trend analyses, mixed plantations in most cases have no significant effects on biodiversity. Given the moderate positive correlation between the sample size and the occurrence of significant effects, this low frequency of significant effects may be partly explained by the relatively low sample size of the studies included (low power in the statistical analysis), with most studies (78%)

involving <6 replicates. Alternatively, it may be related to the nature of the experiments. At the young age of the plantations monitored (11±9.4 years in average), most mixed stands may not have developed a significantly higher structural complexity than their pure counterparts, that can provide for a higher habitat diversity (Bradford and Kastendick, 2010; Juchheim et al., 2020; Stein et al., 2014). It should also be kept in mind that many tree-diversity experiments were not originally designed to study the effects on biodiversity, but focused primarily on productivity and other indicators of tree performance (Depauw et al., 2024). As a result, the size of the treatment plots with mono-specific or mixed tree communities is often relatively small and therefore not well suited to study the effects on forest-dwelling species such as birds or flying insects, with habitats or activity-ranges that are often substantially larger than the plot size. This may partly explain the low number of studies on certain taxonomic groups and the preponderance of studies on taxa with relatively low mobility, such as soil microbiota and understory plants. In addition, some studies might have focused on mixed plantations of tree species with redundant functional traits, with each of them consequently contributing little to ecosystem properties and functioning. Finally, it is also possible that in some of the studies the biodiversity-ecosystem functioning relationships sustaining forest-related taxa may be primarily driven by abiotic factors, such as climate or soil conditions (influenced, for instance, by previous land-use), rather than by biotic factors like tree species composition (Hooper et al., 2005).

Negative effects of mixed plantations were reported by a variety of studies of different nature (i.e., involving plantations of different ages, evaluating different biodiversity indicators, and focusing on different taxonomic groups). This suggests that, although rare, negative effects may in fact arise under a range of conditions. Yet, in most of these studies (9 out of 11) the mixed plantations under study were two-species mixtures. As we have shown, positive effects of mixing on biodiversity appear to be more frequent in studies with a higher number of species in mixed plantations. Furthermore, 39% of the observations reporting negative effects stemmed from a single experiment with young plantations (0–4 years) that was repeatedly surveyed in different studies evaluating soil microbiota diversity (DaSilva et al., 2012; Bini et al., 2018; Pereira et al., 2021; Santana et al., 2021). The experiment had been established on lands managed for nearly 50 years as pure eucalypt plantations. An additional 17% of the observations indicating negative effects of mixing also stemmed from plantations established on former agricultural or clay extraction sides, and focused on soil microbial diversity. At these sites with long-term intensive land use, there may have been a much reduced pool of species that could potentially respond to a more diverse habitat in a short time (Jangid et al., 2011).

4.2. Indicators

Both the trend analyses and the meta-analyses indicate a higher sensitivity of diversity indices than of species richness to mixed plantations. This may be related to aspects of the sampling process. Theoretically, both richness and evenness in the community of forest-related taxa should increase as a result of mixed plantations, due to an enhancement in habitat heterogeneity and increased overall resource availability (Hooper et al., 2005; Ampoorter et al., 2020; Juchheim et al., 2020). However, it is possible that common sampling techniques are less sensitive to changes in richness than in evenness, as newly established species in the mixed plantations might initially show lower abundances, making them less likely to be detected (Gotelli and Colwell, 2001). In addition, the low plot sizes commonly used in tree diversity experiments may often lead to underestimations of species richness, as the species richness measured in experimental conditions often falls short from the saturation point (Hill et al., 1994). Meanwhile, the patterns associated with functional and phylogenetic diversity should be interpreted cautiously given the lower sample sizes for these indices, especially since they did not allow for meta-analyses. However, the higher effects on phylogenetic diversity may be due to this indicator more accurately reflecting the complementarity in habitat provision by the tree community, compared to richness or diversity indices. According to theory, an array of forest-dwelling species with high trait diversity would be required to occupy the variety of niches created in mixed-species plantations. Since functional and structural traits are the result of evolutionary history, functional diversity is often assumed to be related to phylogenetic diversity (Tucker and Emmingham, 1977; Castagneyrol et al., 2014; M. Cadotte et al., 2017). As a consequence, phylogenetic diversity, rather than species numbers and relative abundances, may better describe the higher functional diversity of the forest-related taxa in mixed plantations.

4.3. Moderators

The higher effects of mixed plantations observed in studies from tropical climates when compared to temperate and continental climates should be considered cautiously given the low sample size for the tropical climate type, and the lack of sufficient data for meta-analyses to confirm this trend. However, the pattern may simply reflect the faster growth of plantations in tropical regions. At the young age at which most surveys took place, the structural and functional differentiation of mixed plantations from pure plantations, which eventually should lead to higher biodiversity, may have already begun to manifest in tropical regions, whereas in colder climates, this process may take longer (Ehbrecht et al., 2021). Additionally, the intrinsic higher biodiversity of tropical forests may offer a higher chance for functionally distinct species occupying the increased variety of niches created in mixtures (Cao et al., 2021).

This may also partly explain the decreasing effects of mixing with increasing plantation age indicated by our results. At first glance, this trend may seem surprising, as the diversity of structures and functions in mixed plantations would be expected to increase with plantation age (Bradford and Kastendick, 2010; Juchheim et al., 2020). However, the significant effects indicated by the meta-analysis for plantations in the age class 0 to 5 years are derived almost exclusively from studies in tropical regions, where positive effects at early plantations ages should be more likely due to higher growth rates. Unfortunately, the low number of studies (n=7) prevents a reliable assessment of the influence of the climate type within this age class. Furthermore, most plantations in the age class 5 to 20 years may be experiencing canopy closure and high stand density, leading to limited light availability in the understory, and consequently, low structural complexity and species diversity (Halpern and Spies, 1995; Hedwall et al., 2019). Additionally, considering the relatively narrow and young age of plantations in the >20 years' age class (26±3 years on average), as well as the low sample size of the meta-analysis for this age class, more studies involving older plantations (e.g., over 30 years) would be necessary to fully capture the processes occurring at more advanced developmental stages. Research on older stands has provided valuable insights into biodiversity patterns in mixed forests, yet such studies have often been conducted in previously managed forests, resulting in less controlled treatments. This leads to an increased variability and lack of detailed information on stand origin and age, which was often the reason for exclusion from this review. Furthermore, these studies often compare monocultures with two-species mixtures rather than examining a gradient of tree species diversity. As a result, their findings are often determined by site-specific environmental conditions and species identity, rather than by tree species diversity, which is often reflected in a lower occurrence of positive effects of mixed vs pure forests (Schuldt et al., 2022; Schauer et al., 2023; Glatthorn et al., 2023; Wenglein et al., 2024; Wildermuth et al., 2024a).

The meta-analyses and trend analyses consistently reported stronger effects of mixed plantations with a higher number of tree species. This aligns with the main theories and synthesis of evidence on the relationship between tree species diversity and ecosystem functioning (i.e. redundancy, insurance, sampling effect, complementarity) (Tilman et al., 1997; Loreau, 2000; Hooper et al., 2005; Forrester and Bauhus, 2016), suggesting they are also applicable to the effects of tree diversity on forest-related biodiversity. In particular, the higher frequency of negative effects of mixed plantations observed in two-species mixtures may be due to a strong reliance of forest-related taxa on one of the tree species from the mixture. In the mixture, the relative abundance of that tree species would be lower than in the monoculture, which may reduce the ecological functions it provides, while creating spatial isolation among its individuals. This may eventually lead to less diverse communities of dependent taxa (Yguel et al., 2011; Van der Plas et al., 2016). These results highlight the importance of accounting for the number of species mixed when evaluating the overall effects of mixed plantations on biodiversity. With few studies providing this information, some of our comparisons among different moderator classes had to be limited to studies with two-species mixed plantations to prevent biases. Eventually, different patterns may emerge when including studies with more than two species, or when consistently accounting for the influence of the number of species across different types of studies. In general, consistent positive effects seen in controlled experiments with multiple-species mixtures (Fornoff et al., 2019; Skarbek et al., 2020; Guo et al., 2021; Matevski and Schuldt, 2021; Wang et al., 2019; Vázquez-González et al., 2024) seem to contrast with often mixed or inconclusive results of observational studies limited to two-species mixtures (Schuldt et al., 2022; Schauer et al., 2023; Glatthorn et al., 2023; Wenglein et al., 2024; Wildermuth et al., 2024a). This apparent contrast highlights the value of controlled experimental approaches, suggesting they offer a clearer understanding of biodiversity impacts, as these are less confounded by species identity or stand variability (Eisenhauer et al., 2016).

Both the trend analyses and the meta-analyses indicate that mixed plantations combining species in similar abundances have only slightly stronger effects on biodiversity, than those with uneven species abundances. However, the meta-analyses revealed significant effects only for plantations with even species abundances. This suggests that not only the number of tree species in mixed plantations is relevant for forest-related biodiversity, but also their relative abundance. In mixed plantations with uneven species abundances, the functions expected from the less abundant species may be performed at a lower intensity, which may limit the potential benefits of mixing, whereas the opposite would occur in mixed plantations with even species abundances (Petchey and Gaston, 2006).

Theoretically, mixing species with different traits may help achieving higher ecosystem functioning and structural complexity, leading to higher biodiversity. We expected that mixed plantations composed of both conifers and broadleaves would achieve higher biodiversity levels, based on the assumption that the underlying differences in structural and functional traits among both groups (e.g. leaf structure, root development, wood properties) (Canadell et al., 1996; Shmulsky and Jones, 2011) would contribute to a higher niche diversity (Ozanne, 1999; Ampoorter et al., 2020; Juchheim et al., 2020). Nevertheless, our analyses indicate consistently that mixing conifers and broadleaves does not necessarily result in higher biodiversity. In fact, the trend analysis shows that significant effects of mixing are less frequent when both conifers and broadleaves are mixed, compared to when only conifers or broadleaves are mixed. This is consistent with studies indicating structural and functional trait convergence among conifer and broadleaved species (Reich et al., 1997; Zhang et al., 2020; Higham et al., 2022). Therefore, higher functional diversity may be better achieved when selecting species based on specific, targeted traits, rather than simply mixing broad taxonomic groups.

4.4. Taxonomic/functional groups

Due to the lack of data for litter microbiota, soil mesofauna, and birds for meta-analyses, we were only able to corroborate the positive trends suggested by the trend analyses for understory plants, soil microbiota, and above-ground arthropods. Moreover, the meta-analyses only confirmed significant effects for understory plants. However, the positive trends depicted by both methods for understory plants, soil microbiota, and above-ground arthropods were consistent in each case in which the comparisons were possible. Additionally, further studies that did not meet our inclusion criteria or were published subsequent to our search, consistently support the trends observed for a variety of above- and belowground arthropod groups, including hemiptera (Fornoff et al., 2019), hymenoptera (Fornoff et al., 2019; Skarbek et al., 2020; Guo et al., 2021), spiders (Matevski and Schuldt, 2021), lepidoptera (Wang et al., 2019), as well as for birds (May-Uc et al., 2020; Vázquez-González et al., 2024).

The variation in the sensitivity of the diversity of the different taxonomic/functional groups to mixed plantations, as shown by the trend analyses, seems to reflect the strength of these groups' interactions with the tree community, as well as their dependence on it. Tree structure and composition directly determines the availability of nesting and foraging resources for bird species (MacArthur and MacArthur, 1961). Since mixed forests often exhibit higher structural complexity (Juchheim et al., 2020), it is not surprising that birds show the highest sensitivity to mixed planting. This result aligns with previous studies that demonstrate strong relationships between tree and bird species diversity (James and Wamer, 1982; Beason et al., 2023). Similarly, canopy structural heterogeneity and tree species composition are key drivers of arthropod composition in forests (Schaffers et al., 2008; Wildermuth et al., 2024b). Tree species composition also influences leaf litter composition and production, affecting its chemical properties and decomposition rates, which in turn impact the litter microbial community composition (Scherer-Lorenzen et al., 2007; Jacob et al., 2010). Additionally, the overstory community influences understory plant composition both directly, through direct seed dispersal and by mediating factors like permeability to sunlight, water availability, nutrient cycling, and soil characteristics, among others, and indirectly, by attracting specific seed-dispersing animals (Oliver and Larson, 1996). Thus, the frequent effects of mixed plantations on the diversity of these groups (i.e., above-ground arthropods, litter microbiota, and understory plants) are not surprising.

In particular, the comparatively higher proportion of negative response to mixing shown by above-ground arthropods stemmed from two studies that have little in common, apart from focusing on specific taxa that are dependent on particular tree species or conditions prevailing in monocultures. The first case involved heliophile beetle species associated with higher light abundance in monocultures due to a sparse, mono-layer canopy (Quinto et al., 2021), while the second case involved staphylinids apparently dependent on abundance of *Fraxinus excelsior*, which was highest in pure plantations of this native species, as opposed to the mixed plantations that included non-native conifer species (Oxbrough et al., 2012).

The changes introduced by mixed plantations in the above-ground structure and leaf litter composition may often occur in the short to medium term. As a result, the responses of both above-ground and litter-dwelling organisms to mixing are evident even at the generally young age of the plantations addressed in the studies included here. However, ecosystem properties like soil chemical and physical characteristics may require more time to respond to the establishment of mixed plantations, since these processes are often mediated by long-term interactions between plant species, soil organisms, and environmental conditions (Iwashima et al., 2012; Gunina et al., 2017). The lower response of soil microbiota and particularly soil mesofauna shown by our results, which is consistent with findings from regionally-replicated tree diversity experiments (Depauw et al., 2024), may simply reflect the early successional stages of the plantations addressed, at which point such changes may not have yet fully occurred.

Finally, our evidence base showed a significant bias towards studies addressing soil microbiota, understory vegetation, and above-ground arthropods, while most other groups are underrepresented, limiting the ability to perform specific meta-analyses for them. Moreover, several groups, particularly vertebrates other than birds, or saproxylic species, were absent. This indicates the general patterns identified should be interpreted with caution, as the inclusion of underrepresented or absent groups in future studies may significantly affect our conclusions.

4.5. Conclusions

This study represents the first comprehensive and systematic synthesis of scientific evidence on the effects of mixed tree plantations on biodiversity. Our findings indicate that mixed-species plantations generally have a positive effect on biodiversity, while negative effects are rare. Nevertheless, in most cases examined, mixed plantations had no statistically significant impact on biodiversity. Therefore, when establishing mixed plantations, it is important to focus on the conditions that maximize their benefits. Specifically, mixed plantations are most effective to foster biodiversity when combining more than two species, and when the component species are mixed in even proportions, which should maximize complementarity effects in habitat provision. Additionally, mixed-species plantations appear to be more effective in enhancing biodiversity in tropical climates. Among taxonomic groups, the strongest biodiversity effects are observed for birds, litter microbiota, and understory plants, although statistical evidence supports positive effects only for the latter.

Furthermore, the variability in the effects of mixed plantations associated to the different types of studies and taxa highlights the importance of considering the potential biases in our evidence base. Despite the growing body of evidence on the effects of mixed plantations on biodiversity, further studies are needed to address critical gaps while enabling more detailed syntheses focused on specific regions, forest types, and taxonomic groups relevant for management. In particular, more studies conducted in tropical and continental climates, covering taxonomic groups other than plants, arthropods, and soil microbiota, as well as older plantations (>30 years), are required. Additionally, research assessing indicators of functional and phylogenetic biodiversity would provide deeper ecological insights. Such targeted reviews would allow to address groups or conditions that require more complex experimental designs. For instance, studying the effects of mixed plantations on larger vertebrates or other mobile species with larger spatial requirements would require experiments at larger spatial scales with plot sizes sufficient to capture the responses of these species groups.

Moreover, studies investigating the biodiversity effects of mixed plantations should report essential information (means, standard deviations, sample sizes) to facilitate their inclusion in meta-analyses, one of the most robust approaches for evidence synthesis. Due to their simplicity, trend analyses allow for the inclusion of a larger number of studies. However, they are subject to potential biases, as they do not account for effect sizes or differences in statistical power among studies. Thus, their results should be interpreted with caution. Tree diversity experiments, such as those within the TreeDivNet network (https://treedivnet.ugent.be/), offer a valuable opportunity to address existing knowledge gaps by systematically testing the effects of tree species richness across well-controlled gradients. With regional replication, balanced and transparent experimental designs, and varying numbers of tree species, these experiments enable a more refined understanding of how biodiversity responds to increasing tree diversity.

Unfortunately, because such studies often focus on gradients of tree diversity rather than explicit comparisons between pure and mixed plantations, they rarely include terms like "pure" or "mixed" in their titles, abstracts, or keywords. Instead, they typically refer to concepts such as "tree diversity." Moreover, the origin of the stands under comparison (e.g., planted vs. natural) is often not emphasized. As a result, terms like "plantation" and related synonyms are frequently omitted. These factors led to the exclusion of several potentially relevant studies from our search, which eventually may have introduced a bias towards studies using more conventional or explicit terminology.

To reduce the risk of such omission-related bias, future systematic reviews should consider a broader selection of search terms, and/or additional search strategies such as citation tracking or the targeted inclusion of studies from established networks like TreeDivNet. In the meantime, and as more studies become available, our findings provide preliminary evidence that increasing tree diversity in plantations can benefit biodiversity. These insights may inform reforestation, landscape restoration, and forest management efforts aimed at enhancing biodiversity outcomes.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111182.

CRediT authorship contribution statement

Klaus Kremer: Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bengt-Gunnar Jonsson:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Trishna Dutta:** Writing – review & editing, Investigation, Data curation. **Mayra Flores Tavares:** Writing – review & editing, Investigation, Data curation. **Jürgen Bauhus:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

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.

Acknowledgements

This work was funded by the Horizon 2020 Program from the European Commission, in the framework of the SUPERB project (Grant agreement ID: 101036849), and partly, by the Alexander von Humboldt Foundation (2021 International Climate Protection Fellowship Programme).

Data availabilityThe data used in this study stems from a set of studies that were selected through a systematic approach. The list of studies with their metadata and further information has been submitted jointly with this manuscript, and can be consulted in the supplementary material (Table S5).

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References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, et al., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259 (4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Ampoorter, E., Barbaro, L., Jactel, H., Baeten, L., Boberg, J., Carnol, M., et al., 2020. Tree diversity is key for promoting the diversity and abundance of Forest-associated taxa in Europe. Oikos 129 (2), 13–146. https://doi.org/10.1111/oik.06290.

Barsoum, N., Fuller, L., Ashwood, F., Reed, K., Bonnet-Lebrun, A.S., Leung, F., 2014. Ground-dwelling spider (Araneae) and carabid beetle (Coleoptera: Carabidae) community assemblages in mixed and monoculture stands of oak (Quercus Robur L./ Quercus Petraea (Matt.) Liebl.) and scots pine (Pinus Sylvestris L.). For. Ecol. Manag. 321 (1), 29–41. https://doi.org/10.1016/j.foreco.2013.08.063.

Bauhus, J., Forrester, D.I., Pretzsch, H., 2017a. Mixed-species forests: The development of a forest management paradigm. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-species Forests: Ecology and Management. Springer, Berlin, Heidelberg, pp. 1–25. https://doi.org/10.1007/978-3-662-54553-9_1.

Bauhus, J., Forrester, D.I., Pretzsch, H., 2017b. From observations to evidence about effects of mixed-species stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.),

Mixed-species forests: Ecology and Management. Springer, Berlin, Heidelgerg, pp. 27–71. https://doi.org/10.1007/978-3-662-54553-9_2.
Beason, R.D., Riesch, R., Koricheva, J., 2023. Investigating the effects of tree species diversity and relative density on bird species richness with acoustic indices. Ecol. Indic. 154, 110652. https://doi.org/10.1016/j.ecolind.2023.110652 (October).
Bini, D., dos Santos, C.A., da Silva, M.C.P., Bonfim, J.A., Cardoso, E.J.B.N., 2018. Intercropping acacia Mangium stimulates AMF colonization and soil phosphatase activity in eucalyptus Grandis. Sci. Agric. 75 (2), 102–110. https://doi.org/10.1590/1678-992X-2016-0337.
Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2021. Introduction to Meta-Analysis, second ed. John Wiley & Sons, Oxford.
Bradford, J.B., Kastendick, D.N., 2010. Age-Related Patterns of Forest Complexity and Carbon Storage in Pine and Aspen–Birch Ecosystems of Northern Minnesota, USA. Can. J. For. Res. 40 (3), 401–409. https://doi.org/10.1139/X10-002.
Cadotte, M.W., Livingstone, S.W., Yasui, S.L.E., Dinnage, R., Li, J.T., Marushia, R., Santangelo, J., Shu, W.S., 2017. Explaining ecosystem multifunction with evolutionary models. Ecology 98 (12), 3175–3187. https://doi.org/10.1002/ecy.2045.
Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48 (5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x.
Campbell, M., McKenzie, J.E., Sowden, A., Katikireddi, S.V., Brennan, S.E., Ellis, S., et al., 2020. Synthesis without Meta-Analysis (SWiM) in Systematic Reviews: Reporting Guideline. BMJ 368, l6890. https://doi.org/10.1136/bmj.l6890.
Canadell, J., Jackson, R.B., Ehleringer, J.B., Mooney, H.A., Sala, O.E., Schulze, E.-D., 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia 108 (4), 583–595. https://doi.org/10.1007/BF00329030.
Cao, K., Condit, R., Mi, X., Chen, L., Ren, H., Xu, W., et al., 2021. Species packing and the latitudinal gradient in beta-diversity. Proc. R. Soc. B-Biol. Sci. 288 (1948), 20203045. https://doi.org/10.1098/rspb.2020.3045 rspb.2020.3045.
Castagneyrol, B., Jactel, H., Vacher, C., Brockerhoff, E.G., Koricheva, J., 2014. Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. J. Appl. Ecol. 51 (1), 134–141. https://doi.org/10.1111/1365-2664.12175.
Cavard, X., Bergeron, Y., Chen, H.Y.H., Pare, D., Laganiere, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. Oikos 120, 1683–1695. http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1600-0706.
DaSilva, C.F., Simoes-Araujo, J.L., da Silva, E.M.R., Pereira, M.G., Freitas, M.S.M., Saggin, O.J., et al., 2012. Arbuscular mycorrhizal fungi and glomalin-soil related protein in degrade areas and revegetated with eucalypt and wattle. Ciênc. Florest. 22 (4), 749–761. https://doi.org/10.5902/198050987556.
De Groote, S., van Schrojenstein, I.M., Sercu, B.K., Boonyaritthichaikij, R., Keely, H., De Beelde, R., …Lens L., 2017. Tree species identity outweighs the effects of tree species diversity and forest fragmentation on understorey diversity and composition. Plant Ecol. Evol. 150 (3), 229–239. https://doi.org/10.5091/plecevo.2017.1331.
Depauw, L., De Lombaerde, E., Dhiedt, E., Blondeel, H., Abdala-Roberts, L., Auge, H., et al., 2024. Enhancing tree performance through species mixing: review of a quarter-century of TreeDivNet experiments reveals research gaps and practical insights. Curr. For. Rep. 10, 1–20. https://doi.org/10.1007/s40725-023-00208-y.
Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M, Zemp, D.C., et al., 2021. Global patterns and climatic controls of Forest structural complexity. Nat. Commun. 12 (1), 519. https://doi.org/10.1038/s41467-020-20767-z.
Eisenhauer, N., Barnes, A.D., Cesarz, S., Craven, D., Ferlian, O., Gottschall, F., et al., 2016. Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. J. Veg. Sci. 27 (5), 1061–1070. https://doi.org/10.1111/jvs.12435.
Fornoff, F., Klein, A.M., Blüthgen, N., Staab, M., 2019. Tree diversity increases robustness of multi-trophic interactions. Proc. R. Soc. B 286 (1898), 20182399. https://doi.org/10.1098/rspb.2018.2399.
Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. Curr. For. Rep. 2 (1), 45–61. https://doi.org/10.1007/s40725-016-0031-2.
Gamfeldt, L., Snäll, T., Bagchi, R., JOnsson, M., Gustafsson, L., Kjellander, P., et al., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340. https://doi.org/10.1038/ncomms2328.
Glatthorn, J., Appleby, S., Balkenhol, N., Kriegel, P., Likulunga, E., Lu, J.L., et al., 2023. Species diversity of Forest floor biota in non-native Douglas-fir stands is similar to that of native stands. Ecosphere 14 (7), e4609. https://doi.org/10.1002/ecs2.4609.
Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4 (4), 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x.
Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Fargione, J., 2017. Natural climate solutions. Earth Atmos. Planet. Sci. 114 (44), 11645–11650. https://doi.org/10.1073/pnas.1710465114.
Gunina, A., Smith, A.R., Godbold, D.L., Jones, D.L., Kuzyakov, Y., 2017. Response of soil microbial community to afforestation with pure and mixed species. Plant Soil 412 (1–2), 357–368. https://doi.org/10.1007/s11104-016-3073-0.
Guo, P.F., Wang, M.Q., Orr, M., Li, Y., Chen, J.T., Zhou, Q.S., et al., 2021. Tree diversity promotes predatory wasps and parasitoids but not pollinator bees in a subtropical experimental Forest. Basic Appl. Ecology 53 (June), 134–142. https://doi.org/10.1016/j.baae.2021.03.007.
Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5 (4), 913–934. https://doi.org/10.2307/2269343.
Hedges, L.V., Olkin, I., 2014. Statistical Methods for Meta-Analysis. Academic Press, Orlando.
Hedwall, P.O., Holmstrom, E., Lindbladh, M., Felton, A., 2019. Concealed by darkness: how stand density can override the biodiversity benefits of mixed forests. Ecosphere 10 (8). https://doi.org/10.1002/ecs2.2835.
Higham, T.E., Schmitz, L., Niklas, K.J., 2022. The evolution of mechanical properties of conifer and angiosperm woods. Integr. Comp. Biol. 62 (3), 668–682. https://doi.org/10.1093/icb/icac103.
Hill, J.L., Curran, P.J., Foody, G.M., 1994. The effect of sampling on the species-area curve. Glob. Ecol. Biogeogr. Lett. 4 (4), 97–106. https://doi.org/10.2307/2997435.
Holl, K.D., Aide, T.M., 2011. When and where to actively restore ecosystems? For. Ecol. Manag. 261 (10), 1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004.
Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., et al., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75 (1), 3–35. https://doi.org/10.1890/04-0922.
Huston, M.A., 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of diversity. Oecologia 110, 449–470. https://doi.org/10.1007/s004420050180.
Iwashima, N., Masunaga, T., Fujimaki, R., Toyota, A., Tayasu, I., Hiura, T., et al., 2012. Effect of vegetation switch on soil chemical properties. Soil Sci. Plant Nutr. 58 (6), 783–792. https://doi.org/10.1080/00380768.2012.738183.
Jacob, M., Viedenz, K., Polle, A., Thomas, Frank M., 2010. Leaf litter decomposition in temperate deciduous Forest stands with a decreasing fraction of beech (Fagus Sylvatica). Oecologia 164 (4), 1083–1094. https://doi.org/10.1007/s00442-010-1699-9.
James, F.C., Wamer, N.O., 1982. Relationships between temperate Forest bird communities and vegetation structure. Ecology 63 (1), 159–171. https://doi.org/10.2307/1937041.
Jangid, K., Williams, M.A., Franzluebbers, A.J., Schmidt, T.M., Coleman, D.C., Whitman, W.B., 2011. Land-use history has a stronger impact on soil microbial community composition than aboveground vegetation and soil properties. Soil Biol. Biochem. 43 (10), 2184–2193. https://doi.org/10.1016/j.soilbio.2011.06.022.
Ji, L., Zhang, Y., Yang, Y., Yang, L., Yang, N., Zhang, D., 2020. Long-term effects of mixed planting on arbuscular mycorrhizal fungal communities in the roots and soils of Juglans mandshurica plantations. BMC Microbiol. 20, 30. https://doi.org/10.1186/s12866-020-01987-1.
Juchheim, J., Ehbrecht, M., Schall, P., Ammer, C., Seidel, D., 2020. Effect of tree species mixing on stand structural complexity. Forestry: An International Journal of Forest Research 93 (1), 75–83. https://doi.org/10.1093/forestry/cpz046.
Kornbrot, D., 2014. Point Biserial Correlation. Statistics Reference Online. John Wiley & Sons, Ltd., In Wiley StatsRef https://doi.org/10.1002/9781118445112.stat06227.
Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354 (6309), aaf8957. https://doi.org/10.1126/science.aaf8957.
Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91 (1), 3–17. https://doi.org/10.1034/j.1600-0706.2000.910101.x.
MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. Ecology 42 (3), 594–598. https://doi.org/10.2307/1932254.
Matevski, D., Schuldt, A., 2021. Tree species richness, tree identity and non-native tree proportion affect arboreal spider diversity, abundance and biomass. For. Ecol. Manag. 483 (March), 118775. https://doi.org/10.1016/j.foreco.2020.118775.
May-Uc, Y., Nell, C.S., Parra-Tabla, V., Navarro, J., Abdala-Roberts, L., 2020. Tree diversity effects through a temporal Lens: implications for the abundance, diversity and stability of foraging birds. J. Anim. Ecol. 89 (8), 1775–1787. https://doi.org/10.1111/1365-2656.13245.
Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., et al., 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! Conserv. Lett. 15 (1), e12829. https://doi.org/10.1111/conl.12829.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. Updated edition. John Wiley & Sons, Inc., U.S.
Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., 2009. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. PLoS Medicine 6 (7). https://doi.org/10.1371/journal.pmed.1000097.
Oxbrough, A., French, V., Irwin, S., Kelly, T.C., Smiddy, P., O'Halloran, J., 2012. Can mixed species stands enhance arthropod diversity in plantation forests? For. Ecol. Manag. 270 (April), 11–18. https://doi.org/10.1016/j.foreco.2012.01.006.
Ozanne, C.M., 1999. A comparison of the canopy arthropod communities of coniferous and broad-leaved trees in the United Kingdom. Selbyana 20 (2), 290–298. https://www.jstor.org/stable/41760035.
Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., et al., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. Syst. Rev. 10 (1), 89. https://doi.org/10.1186/s13643-021-01626-4.
Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. Glob. Ecol. Biogeogr. 20 (1), 170–180. https://doi.org/10.1111/j.1466-8238.2010.00592.x.
Pereira, A.P.D., Santana, M.C., Zagatto, M.R.G., Brandani, C.B., Wang, J.T., Verma, J.P., Singh, B.K., Cardoso, E.J.B.N., 2021. Nitrogen-fixing trees in mixed Forest systems regulate the Ecology of fungal community and phosphorus cycling. Sci. Total Environ. 758 (March). https://doi.org/10.1016/j.scitotenv.2020.143711.
Petchey, Owen L., Gaston, Kevin J., 2006. Functional diversity: Back to basics and looking forward. Ecol. Lett. 9 (6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.
Puettmann, K.J., Coates, D., Messier, C.C., 2012. A Critique of Silviculture: Managing for Complexity. Island Press, Washington DC.
Quinto, J., Martinez-Falcon, A.P., Murillo-Pacheco, J.I., Abdala-Roberts, L., Parra-Tabla, V., 2021. Diversity patterns of tropical Epigeal beetle assemblages associated

with monoculture and polyculture plantations with big-leaf mahogany. Neotrop. Entomol. 50 (4), 551–561. https://doi.org/10.1007/s13744-021-00870-6.
R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Reich, P.B., Walters, M.B., Ellsworth, D.S., 1997. From tropics to tundra: global convergence in plant functioning. Proc. Natl. Acad. Sci. U. S. A. 94 (25), 13730–13734. https://doi.org/10.1073/pnas.94.25.13730.
Rohatgi, A., 2022. WebPlotDigitizer - copyright 2010-2022 Ankit Rohatgi. WebPlotDigitizer 2022. https://automeris.io/WebPlotDigitizer/.
Santana, M.C., Pereira, A.P.D., de Souza, A.J., Zagatto, M.R.G., de Araujo, V.L.V.P., Wang, J.T., et al., 2021. Shifts on archaeal community structure in pure and mixed eucalyptus Grandis and acacia Mangium plantations. For. Ecol. Manag. 492, 1192128. https://doi.org/10.1016/j.foreco.2021.119218 (July).
Schaffers, A.P., Raemakers, I.P., Sýkora, K.V., Ter Braak, C.J.F., 2008. Arthropod assemblages are best predicted by plant species composition. Ecology 89 (3), 782–794. https://doi.org/10.1890/07-0361.1.
Schauer, B., Thorn, S., Blaschke, M., Kudernatsch, T., 2023. Conversion of pure spruce to mixed spruce beech stands: effects on alpha and Beta diversity of multiple taxonomic groups. For. Ecol. Manag. 545 (October), 121297. https://doi.org/10.1016/j.foreco.2023.121297.
Scherer-Lorenzen, M., Körner, Ch., Schulze, E.-D., 2005. The functional significance of Forest diversity: The starting point. In: Scherer-Lorenzen, Michael, Körner, Christian, Schulze, Ernst-Detlef (Eds.), Forest Diversity and Function: Temperate and Boreal Systems. Springer, Berlin, Heidelberg, pp. 3–12. https://doi.org/10.1007/3-540-26599-6_1.
Scherer-Lorenzen, M., Bonilla, J.L., Potvin, C., 2007. Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. OIKOS 116 (12), 2108–2124. https://doi.org/10.1111/j.2007.0030-1299.16065.x.
Schuldt, A., Huke, P., Glatthorn, J., Hagge, J., Wildermuth, B., Matevski, D., 2022. Tree mixtures mediate negative effects of introduced tree species on bird taxonomic and functional diversity. J. Appl. Ecol. 59 (12), 3049–3060. https://doi.org/10.1111/1365-2664.14300.
Seddon, N., Chausson, A., Berry, P., Girardin, C.A., Smith, A., Turner, B., 2020. Understanding the value and limits of nature-based solutions to climate change and other global challenges. Philos. Trans. R. Soc. B 375 (1794), 20190120. https://doi.org/10.1098/rstb.2019.0120.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., et al., 2017. Forest disturbances under climate change. Nat. Clim. Chang. 7 (6), 395–402. https://doi.org/10.1038/nclimate3303.
Shmulsky, R., Jones, D., 2011. Hardwood structure. In: Forest Products and Wood Science an Introduction. John Wiley & Sons, Ltd., pp. 79–106. https://doi.org/10.1002/9780470960035.ch5
Simonsen, R., 2013. Optimal regeneration method – planting vs. natural regeneration of scots pine in northern Sweden. Silva Fennica 47 (2). https://www.silvafennica.fi/article/928.
Skarbek, C.J., Noack, M., Bruelheide, H., Härdtle, W., von Oheimb, G., Scholten, T., et al., 2020. A tale of scale: plot but not Neighbourhood tree diversity increases leaf litter ant diversity. J. Anim. Ecol. 89 (2), 299–308. https://doi.org/10.1111/1365-2656.13115.
Staab, M., Blüthgen, N., Klein, A.M., 2015. Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. Oikos 124 (7), 827–834. https://doi.org/10.1111/oik.01723.
Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17 (7), 866–880. https://doi.org/10.1111/ele.12277.
Tate, R.F., 1954. Correlation between a discrete and a continuous variable. Point-Biserial correlation. Ann. Math. Stat. 25 (3), 603–607. https://doi.org/10.1214/aoms/1177728730.
Tedersoo, L., Bahram, M., Cajthaml, T., Põlme, S., Hiieslau, I., Anslan, S., et al., 2016. Tree diversity and species identity effects on soil fungi, protists and animals are context dependent. Multidisciplinary J. Microb. Ecol. 10 (2), 346–362. https://doi.org/10.1038/ismej.2015.116.
Tilman, D., Lehman, C.L., Thomson, K.T., 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proc. Natl. Acad. Sci. U. S. A. 94 (5), 1857–1861. https://doi.org/10.1073/pnas.94.5.1857.
Tucker, G.F., Emmingham, W.H., 1977. Morphological changes in leaves of residual Western hemlock after clear and Shelterwood cutting. For. Sci. 23 (2), 195–203. https://doi.org/10.1093/forestscience/23.2.195.
Vázquez-González, C., Villa-Galaviz, E., Reyes-Hernández, M., Perez-Niño, B., Quijano-Medina, T., Parra-Tabla, V., et al., 2024. Temporal variation in tree diversity effects on birds and its implications for top-down control of insect herbivores in a tropical system. Oecologia 204 (3), 603–612. https://doi.org/10.1007/s00442-024-05514-1.
VanBijsterveldt, C.E.J., Debrot, A., Bouma, T., Maulana, M.B, Pribadi, R., Schop, J., et al., 2022. To plant or not to plant: when can planting facilitate mangrove restoration? Front. Environ. Sci. 9. https://www.frontiersin.org/articles/10.3389/fenvs.2021.690011.
Van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., et al., 2016. Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. Nat. Commun. 7, 11109. https://doi.org/10.1038/ncomms11109 (March).
Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., et al., 2016. Contributions of a global network of tree diversity experiments to sustainable forest plantations. Ambio 45, 29–41. https://doi.org/10.1007/s13280-015-0685-1.
Viechtbauer, W., 2010. Conducting Meta-analyses in R with the Metafor package. J. Stat. Softw. 36 (3), 1–48. https://doi.org/10.18637/jss.v036.i03.
Wang, M.Q., Li, Y., Chesters, D., Anttonen, P., Bruelheide, H., Chen, J.T., et al., 2019. Multiple components of plant diversity loss determine herbivore phylogenetic diversity in a subtropical Forest experiment. J. Ecol. 107 (6), 2697–2712. https://doi.org/10.1111/1365-2745.13273.
Wenglein, R., Jing-Zhong, L., Scheu, S., 2024. The influence of Forest types including native and non-native tree species on soil macrofauna depends on site conditions. Ecol. Evol. 14 (9), e70311. https://doi.org/10.1002/ece3.70311.
Wildermuth, B., Hagge, J., Seifert, C.L., Tjaden, R., Schuldt, A., 2024a. Beneficial effects of native broadleavede forests on canopy beetle diversity are not reduced by admixtrure of non-native conifers. J. Appl. Ecol. 61 (5), 1000–1014. https://doi.org/10.1111/1365-2664.14623.
Wildermuth, B., Penanhat, A., Sennhenn-Reulen, H., Matevski, D., Drescher, J., et al., 2024b. Canopy structure influences arthropod communities within and beyond tree identity effects: insights from combining LiDAR data, insecticidal fogging and machine learning regression modelling. Ecol. Indic. 160, 111901. https://doi.org/10.1016/j.ecolind.2024.111901 (March).
Yguel, B., Bailey, R., Tosh, N.D., Vialatte, A., Vasseur, C., Vitrac, X., et al., 2011. Phytophagy on phylogenetically isolated trees: Why hosts should escape their relatives. Ecol. Lett. 14 (11), 1117–1124. https://doi.org/10.1111/j.1461-0248.2011.01680.x.
Zhang, L., Chen, Y., Hao, G., Ma, K., Bongers, F., Sterck, F.J., 2020. Conifer and Broadleaved trees differ in branch allometry but maintain similar functional balances. Tree Physiol. 40 (4), 511–519. https://doi.org/10.1093/treephys/tpz139.
Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. J. Ecol. 100 (3), 742–749. https://doi.org/10.1111/j.1365-2745.2011.01944.x.