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Species mixing promotes plant biomass accumulation and nutrient cycling in forest plantations

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Mixed-species plantations have been increasingly promoted as a strategy to enhance ecosystem functioning and related ecosystem processes; however, their global impacts on biomass production and nutrient cycling remain uncertain. Here we present a comprehensive meta-analysis based on a random-effects model of 8,450 paired observations from 328 studies spanning diverse climatic zones, stand structures, and silvicultural systems. We demonstrate that species mixing significantly enhances plant biomass and nutrient content compared to monocultures, with positive responses observed across trees, shrubs, litterfall, and both above- and belowground compartments. Mixed-species plantations also increase soil organic carbon, total nitrogen, phosphorus availability, microbial biomass, and leaf nutrient content while maintaining stable soil stoichiometric ratios, collectively reflecting more efficient stand-level nutrient cycling. Importantly, the magnitude of these effects was shaped by climatic and structural contexts, with stronger positive outcomes under warmer and wetter climates, increasing with species richness, and showing unimodal responses to elevation, stand age, and stand density. By synthesizing multi-scale evidence from diverse ecosystems, we reveal that species mixing promotes biomass accumulation, improves nutrient retention, and strengthens biodiversity-nutrient cycling linkages. This study highlights the potential of mixed-species plantations to enhance ecological function, advance forest restoration, and guide plantation management across diverse environmental conditions.

As global forest restoration efforts intensify under frameworks such as the UN Decade on Ecosystem Restoration and the Bonn Challenge, over 350 million hectares of degraded land are targeted for reforestation by 2030^{1,2}. Forest plantations currently cover approximately 7% of global forest area and are projected to expand rapidly³. These plantations aim to provide critical ecosystem services, including carbon sequestration, wood production, and nutrient cycling^{4,5}. However, many programs favor monoculture plantations for their operational simplicity and short-term yields, despite evidence that monoculture plantations account for over 45% of global plantation area and often exhibit poor ecosystem multifunctionality^{3,6,7}. This raises concerns about the capacity

of monocultures to maintain soil fertility, nutrient retention, and other key functions under environmental stress⁸.

In contrast, species mixing in forest plantations has emerged as a promising strategy to enhance productivity and ecosystem functioning^{9,10}. Ecological experiments and observational studies have demonstrated that multispecies plantations often produce higher aboveground biomass (AGB) compared to monocultures, driven largely by niche complementarity and facilitative interactions such as nitrogen fixation and spatial resource partitioning^{11,12}. For instance, mixed-species plantations that include nitrogen-fixing species have been shown to increase soil nitrogen availability, promoting the development of coexisting non-fixing species^{13,14}.

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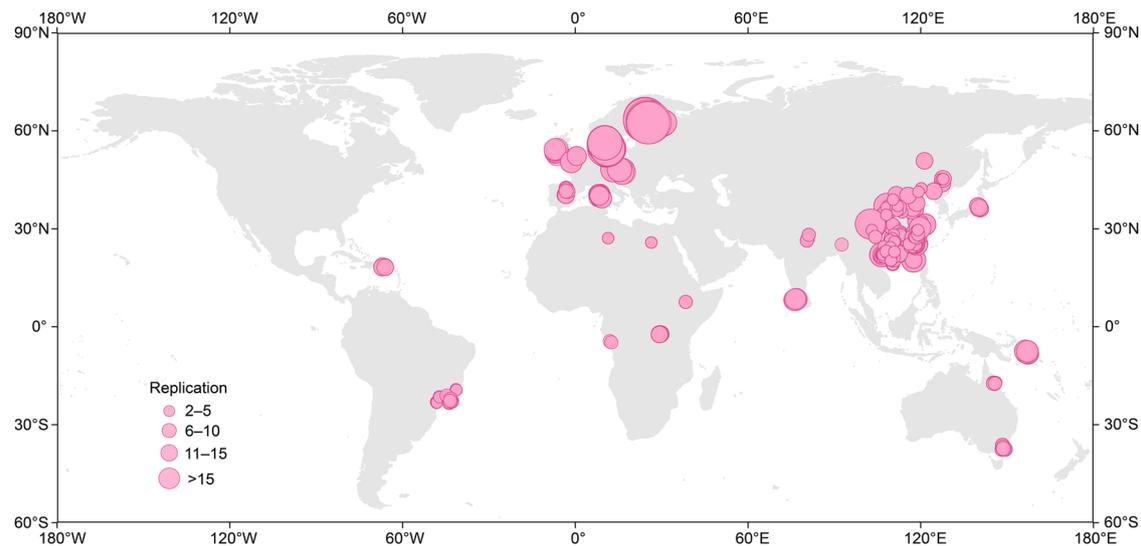


Fig. 1 | Global distribution of the species mixing effects studies included in this meta-analysis. The point sizes indicate the number of effect sizes.

Moreover, increased structural complexity in mixed-species plantations improves water and light use efficiency and may alter nutrient cycling patterns across variable climatic conditions¹⁵. These functional gains demonstrate the potential of species mixing to enhance carbon storage and nutrient retention in plantations across diverse biomes¹⁶.

Nevertheless, empirical evidence regarding the effects of species mixing on nutrient cycling and soil fertility remains inconclusive. While mixed-species plantations often exhibit enriched pools of soil nitrogen and phosphorus compared to monocultures^{17–20}, responses of soil organic carbon (SOC) and microbial biomass are far more variable, showing neutral or even negative effects^{21,22}. This apparent contradiction likely arises because the outcomes are mediated by multiple contextual factors, such as stand developmental stage, species functional composition, edaphic properties, and climatic conditions. Notably, the nutrient accumulation benefits observed in mature plantations are frequently absent in younger stands, and mixtures lacking complementary functional traits may fail to achieve more efficient resource use²³. Moreover, methodological differences (e.g., soil sampling depth, number of tree species) further complicate comparisons. Such heterogeneity underscores the need for a quantitative global synthesis that accounts for these moderators to better understand the circumstances under which species mixing enhances nutrient cycling.

Accurately quantifying the influence of species mixing on both biomass accumulation and nutrient cycling is essential for guiding forest management and restoration policies. Given that nutrient availability fundamentally constrains forest productivity and carbon sequestration^{24,25}, failure to incorporate species diversity considerations risks undermining reforestation outcomes. Furthermore, understanding the conditions under which mixed-species plantations outperform monocultures, in terms of tree productivity and site fertility, can inform species selection and stand design to maximize ecological benefits. To date, however, comprehensive assessments integrating biomass and nutrient dynamics across broad geographical and temporal scales remain scarce, restricting policy- and practice-relevant evidence.

To systematically evaluate species mixing effects in forest plantations, we assembled a global dataset comprising 8450 paired observations that compared monoculture and mixed-species stands (Fig. 1). The data were collected from 17 countries across six continents, spanning diverse climatic regions, plantation types, and silvicultural practices. This global synthesis enabled us to evaluate general patterns while accounting for variation in environmental and management conditions. This study aimed to (1) illustrate and quantify how species mixing influences plant biomass accumulation and nutrient content in forest plantations, and (2) determine the

primary moderators and global trends of plant biomass accumulation and nutrient content in response to species mixing. We postulated that (i) species mixing has positive effects on plant biomass accumulation both aboveground and belowground, as well as nutrient cycling in forest plantations, and (ii) species mixing effects positively correlate with the number of species in the mix and stand age.

Results

Species mixing effects on the biomass of trees, shrubs, herbs, and litterfall

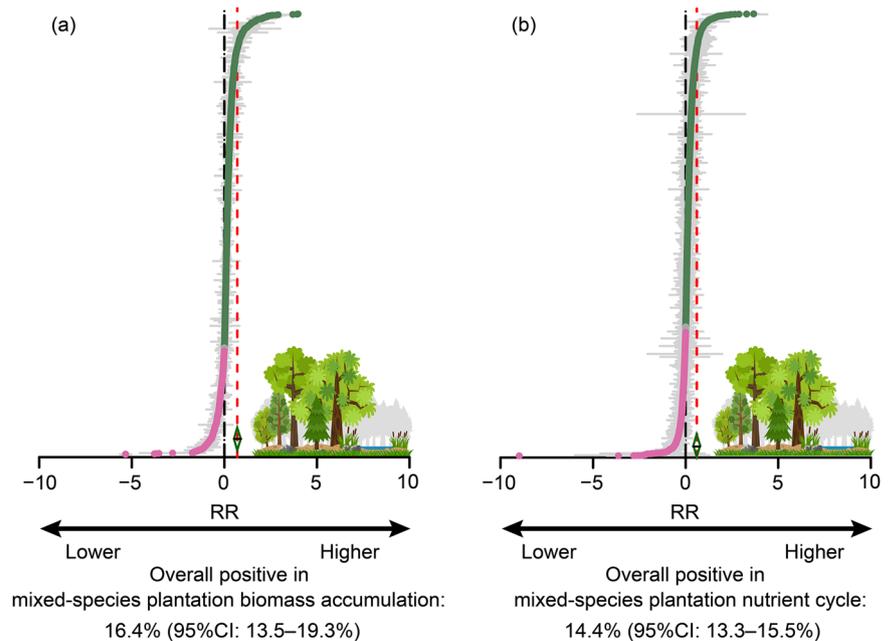
For all of the forest plantations included in this study, species mixing significantly increased the biomass accumulation and nutrient content by 16.4% (back-transformed 95% CI: 13.5–19.3%; Fig. 2a and Supplementary Table 1) and 14.4% (95% CI: 13.3–15.5%; Fig. 2b and Supplementary Table 1). Specifically, in mixed-species plantations, AGB and belowground biomass (BGB) both increased significantly, by 29.0% and 24.2%, respectively. Total tree biomass (TTB) increased by 19.3%, tree aboveground biomass (TAB) by 25.8%, and tree belowground biomass (TBB) by 22.0% (Fig. 3a and Supplementary Table 2). Shrub total biomass (STB) and shrub aboveground biomass (SAB) increased significantly by 31.7% and 84.1%, respectively, while shrub belowground biomass (SBB) showed no significant change. Biomass of herbaceous plants (including herb AGB, HAB; herb belowground biomass, HBB; and herb total biomass, HTB) and total understory vegetation (UVB) also remained unaffected, whereas litterfall biomass (LTB) increased significantly by 36.3% (Fig. 3a and Supplementary Table 2).

Tree morphological traits responded positively to species mixing. Crown length (CL) increased by 12.4%, crown width (CW) by 6.8%, diameter at breast height (DBH) by 7.5%, and tree height by 4.9% (Fig. 3b and Supplementary Table 3). Biomass allocation within trees also shifted. Leaf biomass increased by 13.0%, shoot biomass by 18.0%, stem biomass by 20.9%, root biomass by 14.0%, and stump biomass by 36.3%, but had no significant effect on bark biomass. Coarse root biomass increased significantly by 15.6%, while fine root biomass remained unchanged. Stand volume and mean individual tree volume (MIV) increased by 14.1% and 37.7%, respectively (Fig. 3b and Supplementary Table 3).

Species mixing effects on the nutrient content of soil, litterfall, and tree leaves

Species mixing consistently enhanced key soil nutrient pools and improved nutrient cycling processes, with pronounced effects on both carbon and nitrogen dynamics. In mixed-species plantations, total carbon (TC), SOC,

Fig. 2 | Overall effects of species mixing on plant biomass (a) and nutrient cycling (b) in forest plantations. RR represents response ratios (effect sizes), depicted by dots, with 95% confidence intervals (CI) shown as gray lines. Dot colors indicate the direction of the effect size: green for positive effects, pink for negative effects, and gray for no effects. The black dashed line indicates RR = 0, while the overall effect size is represented by the red dashed line and the green diamond (with 95% CI in the black line).



soil carbon stock (SCS), and microbial biomass carbon (MBC) increased by 10.1%, 20.2%, 29.2%, and 14.2%, respectively (Fig. 4a and Supplementary Table 4). Total nitrogen (TN), available nitrogen (AN), and microbial biomass nitrogen (MBN) increased by 14.7%, 22.0%, and 22.3%, respectively. For phosphorus, total and available phosphorus (TP and AP) increased by 7.8% and 24.9%, while potassium availability improved as total and available potassium (TK and AK) increased by 12.3% and 10.2%. Similarly, soil organic matter (SOM) content increased by 15.5%. Notably, despite these widespread increases, species mixing did not disrupt the overall stoichiometric balance of soil. There were no significant effects on microbial biomass phosphorus (MBP), the carbon to nitrogen ratio (C:N), carbon to phosphorus ratio (C:P), and microbial carbon to nitrogen ratio (MBC:MBN) (Fig. 4a and Supplementary Table 4).

Mixed-species stands also altered nutrient content in plant tissues, particularly in litterfall and leaves, with implications for nutrient return and resorption. Nitrogen and potassium content in litterfall (LTN and LTK) increased substantially by 42.1% and 46.7% respectively. In contrast, carbon and phosphorus content (LTC and LTP), as well as litterfall stoichiometry, remained unchanged (Fig. 4b and Supplementary Table 5). In tree leaves, nitrogen and phosphorus content (LN and LP) increased by 6.8% and 9.2%, whereas the carbon to nitrogen ratio (LC:LN) declined significantly by 18.8%, suggesting improved leaf nutrient status. No significant changes were found in leaf carbon or potassium content (LC and LK), nor in leaf carbon to phosphorus and nitrogen to phosphorus ratios (LC:LP and LN:LP) (Fig. 4b and Supplementary Table 5).

Moderators of species mixing effects on plant biomass and nutrient content

Meta-regression analyses revealed that, at the whole-stand level, the positive effects of species mixing on biomass and nutrient content increased progressively with rising mean annual temperature (MAT), mean annual precipitation (MAP), and species richness (Figs. 5 and 6). The relationship between the positive effect of species mixing on biomass and elevation, stand age, and stand density each followed a unimodal pattern, which peaked at ~840 m, ~28 years, and ~2500 stems ha⁻¹, respectively. Beyond these points, the effects shifted to negative at ~1680 m, ~55 years, and ~5000 stems ha⁻¹. Similarly, the positive effects of species mixing on nutrient contents showed unimodal relationships with elevation and stand density, reaching a peak at ~1500 m and ~3300 stems ha⁻¹, and turning negative at 3000 m and ~6700 stems ha⁻¹. In contrast, the positive effect of species mixing on

nutrient contents increased gradually with stand age and stabilized after ~54 years (Figs. 5 and 6).

Discussion

Species mixing enhances tree biomass accumulation in forest plantations

Our results provide robust evidence that species mixing substantially promotes biomass accumulation in forest plantations, supporting our first hypothesis. This is consistent with previous studies that found a positive relationship between biodiversity and productivity in forest ecosystems^{26–29}. The strongest effects were observed in trees, with mixed-species stands showing significant increases in TTB (+19.3%), TAB (+25.8%), and TBB (+22.0%). These gains coincided with pronounced enhancements in morphological traits such as CL (+12.4%), CW (+6.8%), DBH (+7.5%), and tree height (+4.9%), revealing a marked reconfiguration of stand structure driven by species mixing. Such synchronous increases in structural traits and AGB indicate that mixtures supported greater crown surface development and photosynthetic investment relative to monocultures. The enlarged crown dimensions and increased vertical growth suggest that mixed-species plantations develop more complex, vertically stratified canopies that optimize light capture and reduce self-shading^{30,31}. This vertical niche differentiation among coexisting species serves as a key mechanism driving overyielding by expanding the photosynthetically active space, a concept supported by empirical and modeling studies^{30,32}. A growing body of field evidence demonstrates that mixed-species plantations exhibit pronounced canopy stratification, enhanced crown complementarity, and more efficient vertical partitioning of light, thereby increasing stand-level light-use efficiency^{33,34}. Structural measurements from long-term experiments show that species differ consistently in preferred canopy positions and crown architectures, enabling multilayered canopies that capture a broader range of light environments than monocultures^{30,32,35}. Considering this foundation, our results further support the interpretation that structural reorganization under species mixing is directly coupled with tree-level biomass increases, providing evidence that mixtures increase stand-scale productive volume rather than simply shifting biomass allocation. Together, these findings bridge ecological theory with practical forest management by revealing how species mixing reshapes canopy structure to improve ecosystem-level performance.

Belowground, species mixing altered biomass allocation patterns, notably increasing coarse root biomass while maintaining fine root biomass

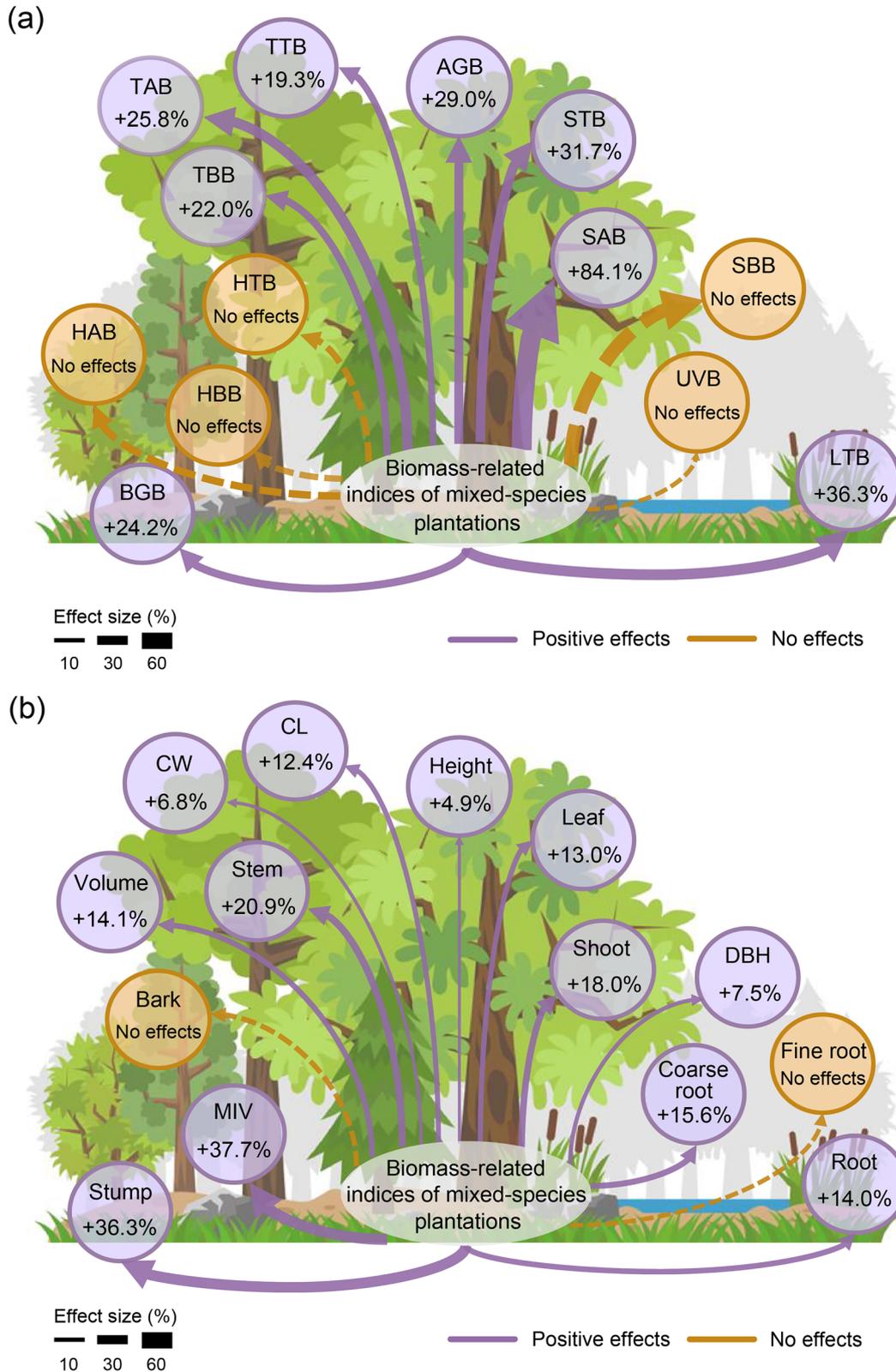
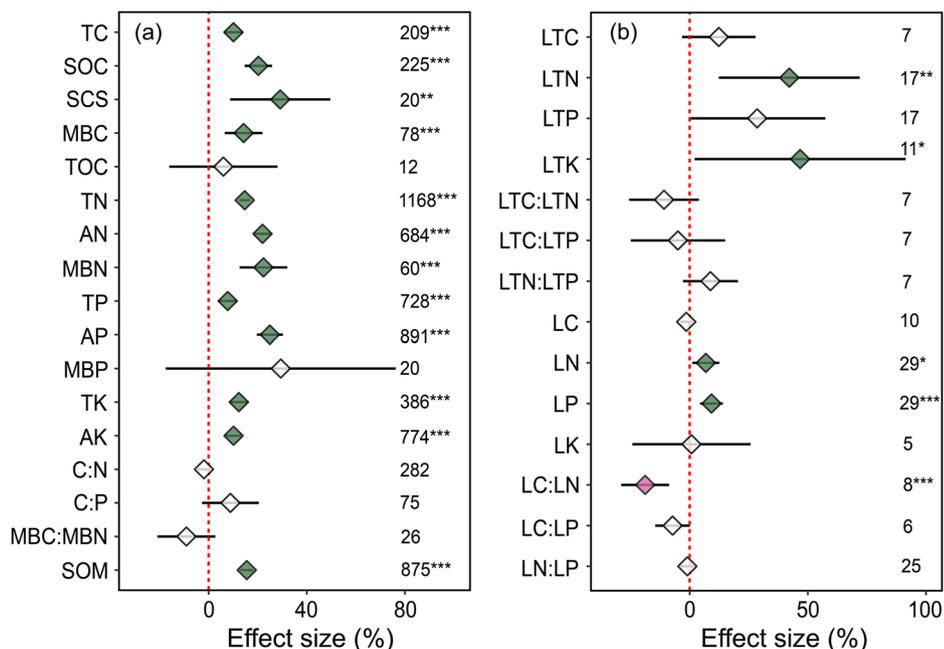


Fig. 3 | Species mixing effects on the biomass of trees, shrubs, herbs, and litterfall (a), as well as on the growth indicators and component biomass of trees (b) in forest plantations. The data presented in the circle is the mean effect size (RR). No effects indicate RR = 0. Purple circles with solid arrows represent positive effects, and golden-brown circles with dashed arrows represent no (neutral) effects. The thickness of the arrow represents the magnitude of the effect. AGB aboveground

biomass, BGB belowground biomass, TTB tree total biomass, TAB tree aboveground biomass, TBB tree belowground biomass, STB shrub total biomass, SAB shrub aboveground biomass, SBB shrub belowground biomass, HTB herb total biomass, HAB herb aboveground biomass, HBB herb belowground biomass, UVB understory vegetation biomass, LTB litterfall biomass, CL crown length, CW crown width, DBH diameter at breast height, MIV mean individual volume.

Fig. 4 | Species mixing effects on soil nutrient content (a), litterfall nutrient content, and leaf nutrient content (b) in forest plantations. Effect sizes are presented as the mean \pm 95% confidence interval (CI). The dashed red line represents RR = 0. Green diamonds represent positive effects, pink diamonds represent negative effects, and white diamonds represent no (neutral) effects. Numbers beside each ecological attribute represent the number of independent observations. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. TC total carbon, SOC soil organic carbon, SCS soil carbon stock, MBC microbial biomass carbon, TOC soil total organic carbon, TN total nitrogen, AN available nitrogen, MBN microbial biomass nitrogen, TP total phosphorus, AP available phosphorus, MBP microbial biomass phosphorus, TK total potassium, AK available potassium, C:N soil carbon to nitrogen ratio, C:P soil carbon to phosphorus ratio, MBC:MBN microbial carbon to nitrogen ratio, SOM soil organic matter, LTC litterfall carbon content, LTN litterfall nitrogen content, LTP litterfall phosphorus content, LTK litterfall potassium content, LTC:LTN litterfall carbon to nitrogen ratio, LTC:LTP litterfall carbon to phosphorus ratio, LTN:LTP litterfall nitrogen to phosphorus ratio, LC leaf carbon content, LN leaf nitrogen content, LP leaf phosphorus content, LK leaf potassium content, LC:LN leaf carbon to nitrogen ratio, LC:LP leaf carbon to phosphorus ratio, LN:LP leaf nitrogen to phosphorus ratio.



unchanged. This finding aligns with the theory of spatial root niche complementarity, where species partition soil resources at different depths to minimize competition and enhance collective resource uptake^{36,37}. The substantial increase in stump biomass (+36.3%) further indicates reinforced structural support accompanying intensified aboveground growth. It is worth noting that STB and SAB increased by 31.7% and 84.1%, respectively. This selective increase in shrub biomass, combined with stable herb biomass, demonstrates that productivity enhancement extended beyond the tree layer and occurred primarily in the midstory. Given the lack of change in SBB and the enhanced soil nutrient availability detected in mixtures, shrub growth likely proceeded without additional belowground investment, indicating that resource availability was sufficient to support aboveground expansion. This pattern suggests that the benefits of species mixing propagate vertically through the stand profile, enabling shrub biomass to accumulate without displacing herb biomass or intensifying belowground competition. Combined, these findings reveal that species mixing enhances biomass accumulation not simply by increasing resource availability but through orchestrated changes in forest stand architecture and biomass allocation. This multi-layer response refines current understanding of mixture overyielding by indicating that increased productivity arises from the integration of enhanced tree growth, increased coarse root support, and additional carbon storage within the shrub layer. Our study thus highlights the potential of species-diverse planting strategies to sustainably enhance forest productivity, aligning ecological insights with silvicultural objectives.

Species mixing improves nutrient cycling in forest plantations

Our findings demonstrate that species mixing substantially elevates soil nutrient stocks and cycling processes, confirming and expanding prior evidence linking biodiversity to ecosystem processes^{37–39}. Significant increases in TC, SOC, MBC, and TN reflect enhanced carbon and nitrogen sequestration in mixed-species plantations, which indicates that more diverse stands promote both greater nutrient accumulation and more dynamic nutrient processing. These changes signal not only augmented nutrient inputs but also potentially accelerated nutrient turnover mediated by a more diverse and active soil microbial community.

The observed increases in MBN (+22.3%) and AN (+22.0%) further suggest that species mixing fosters microbial processes that enhance nitrogen mineralization and availability. A likely mechanism is the improved litterfall resource environment created by mixtures, which supply both higher quality and more heterogeneous organic inputs. This interpretation is supported by the significant enrichment of LTN (+42.1%) and LTK (+46.7%), coupled with increased LN (+6.8%) and LP (+9.2%). Together, these patterns align with theoretical expectations that greater functional diversity in litterfall traits enhances the diversity and quality of nutrient inputs, thereby sustaining soil fertility⁴⁰.

Despite these pronounced nutrient enhancements, the lack of significant shifts in soil C:N and C:P indicates that species mixing maintains overall soil stoichiometric balance. Such stability suggests that nutrient enrichment in mixed-species plantations does not disrupt key elemental ratios that regulate microbial metabolism and plant nutrient uptake⁴¹. This stoichiometric stability may be critical for maintaining long-term productivity. Our results also indicate that phosphorus and potassium pools benefit from species mixing, with TP and AP increasing by 7.8% and 24.9%, and TK and AK by 12.3% and 10.2%, respectively. These responses extend the influence of species mixing to multiple macronutrients and highlight that mixtures improve not only carbon and nitrogen dynamics but also the availability of elements that frequently limit forest growth^{42,43}. The enhanced nutrient availability likely facilitates sustained tree growth and supports the higher biomass accumulation observed in mixed plantations. Collectively, these results reveal a positive feedback mechanism in which species mixing enhances litterfall quality and diversity, boosts microbial biomass and activity, thereby accelerating nutrient cycling and soil accumulation. This feedback provides empirical support for our second hypothesis, which states that species mixing benefits are influenced by stand characteristics and environmental factors, thereby promoting the application of biodiversity-ecosystem function theory in plantation management practice.

Factors modulating the magnitude of species mixing effects

Meta-regression revealed that species mixing effects on biomass accumulation and nutrient content were strongly modulated by climatic

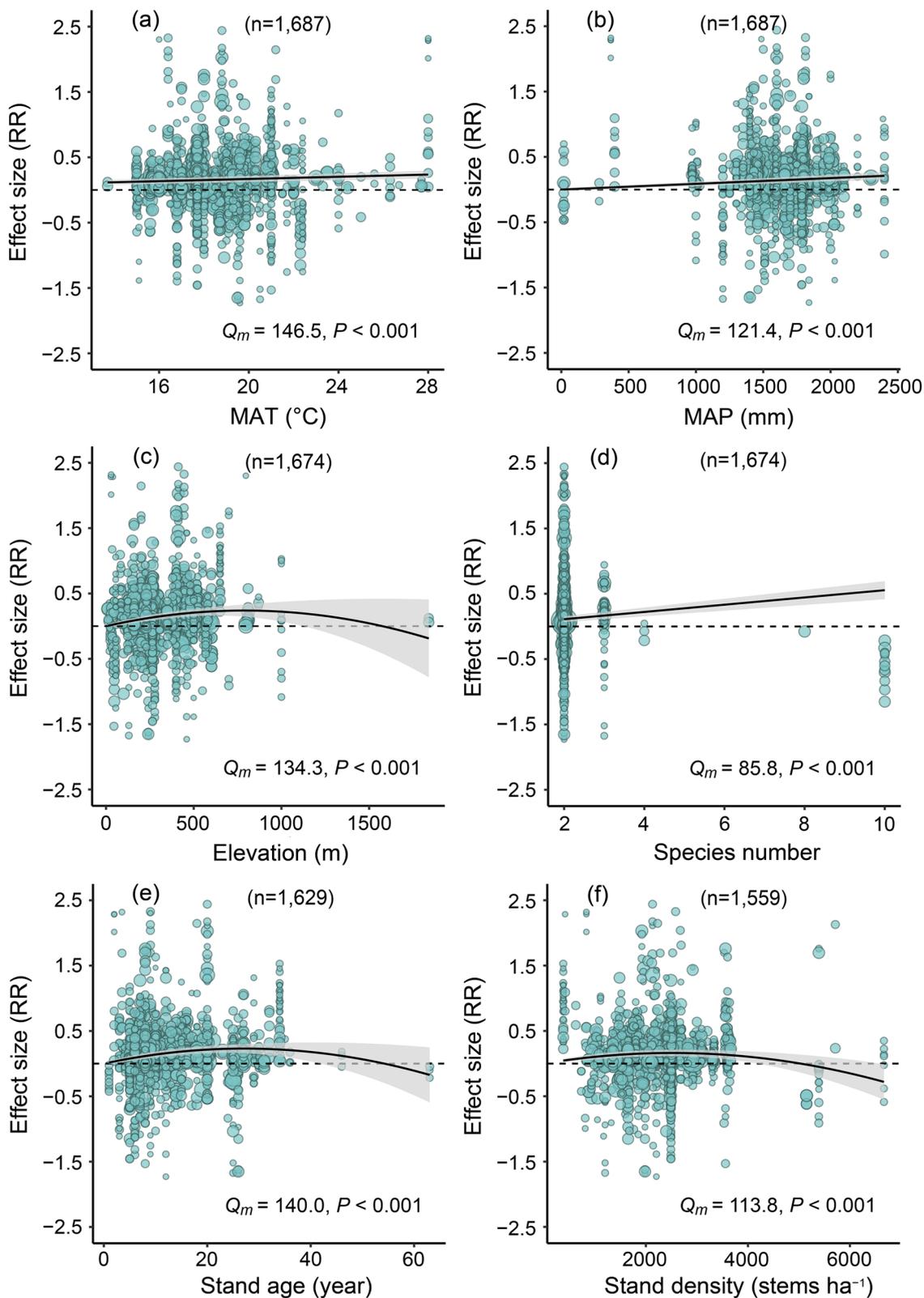


Fig. 5 | Moderators that affect species mixing effects on plant biomass in forest plantations. Variation in species mixing effects on plant biomass in forest plantations as a function of mean annual temperature (a, MAT), mean annual precipitation (b, MAP), elevation (c), tree species number (d), stand age (e), and stand

density (f). RR, log response ratio. RR = 0, dashed black line; predicted mean effect size (with 95% CI in light gray stripe), black lines. Bubbles represent the individual case studies. Bubble sizes are proportional to the weights of the observations.

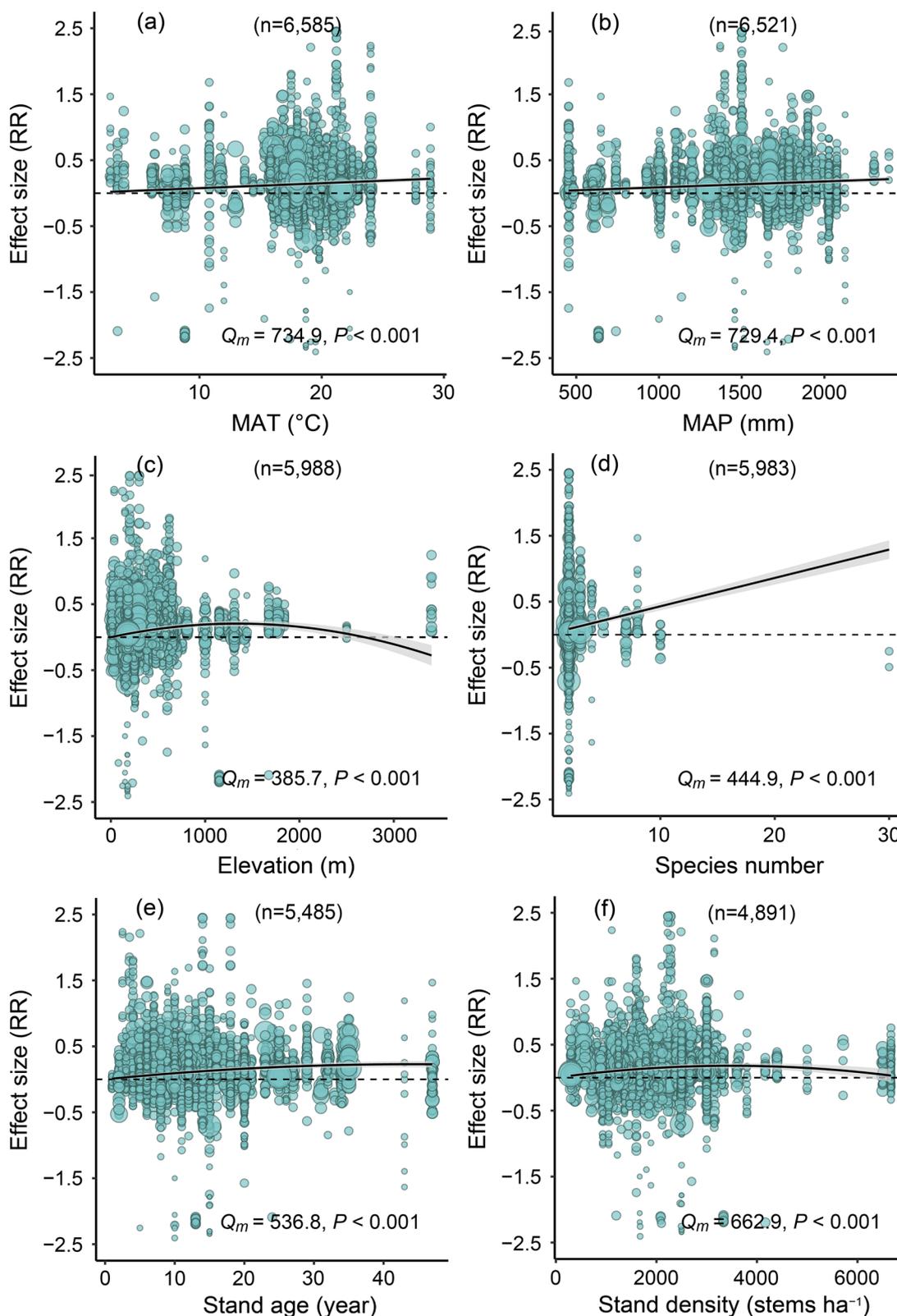


Fig. 6 | Moderators that affect species mixing effects on plant and soil nutrients in forest plantations. Variation in species mixing effects on plant and soil nutrients in forest plantations as a function of mean annual temperature (a, MAT), mean annual precipitation (b, MAP), elevation (c), tree species number (d), stand age (e), and

stand density (f). RR, log response ratio. RR = 0, dashed black line; predicted mean effect size (with 95% CI in light gray stripe), black lines. Bubbles represent the individual case studies. Bubble sizes are proportional to the weights of the observations.

conditions, elevation, and stand structure, supporting our second hypothesis. Mixing effects increased significantly with MAT and MAP, indicating that climates with higher energy availability and moisture supply favor biomass accumulation in mixed-species plantations^{11,44}. These positive slopes suggest that longer growing periods and faster nutrient turnover magnify complementarity under warm and humid climates, thereby reinforcing overyielding. The absence of performance saturation along thermal and moisture gradients further implies that productivity gains from species mixing may intensify rather than stabilize with increasing temperature and water supply, highlighting considerable potential for mixed plantations in high rainfall and warm regions (Figs. 5a, b and 6a, b). Along elevation, however, the trend shifted from positive to neutral and ultimately negative, demonstrating a unimodal rather than monotonic relationship. Complementarity evidently strengthens when moderate stress promotes niche segregation, but declines when cold limitation shortens assimilation windows and restricts metabolic functioning (Figs. 5c and 6c). The transition from positive to negative effect at high elevation thus represents a practical ecological boundary, suggesting that mixed species plantations are most favorable in low to mid elevation contexts, whereas performance may weaken or reverse in cold upland zones. These gradients collectively indicate that the benefits of mixing emerge only when resource availability, physiological capacity, and environmental stress operate within compatible ranges.

Stand level attributes also governed variation in effect size. Species number showed a positive association with mixing benefits, consistent with increased complementarity, where functional variation broadens resource use^{12,45}. Stand age exhibited a unimodal pattern, with early enhancement driven by crown stratification and physiological differentiation that later diminished under intensified competition for light and soil resources. The approximate biomass peak occurs around 28 years (close to the conclusion of previous studies, which peaked at ~25 years)¹¹, and the nutrient peak occurs near 54 years. Therefore, interventions such as thinning or regeneration at these stages can maintain complementarity and prevent the mixed-breed advantage from declining in later stages. Stand density presented a similar unimodal pattern, with the highest gains under moderate crowding that promotes competitive release and resource redistribution. Maintaining density near 2500 to 3300 stems per hectare appears to optimize mixing benefits, whereas densities exceeding 5000 stems per hectare increase competitive stress and may shift mixture advantage toward neutral or negative effects. These structural attributes function as filters that determine how efficiently trait diversity translates into productivity. Taken together, these patterns show that the benefit of species mixing does not hold everywhere, but arises only when climate, elevation, age, and density fall within a zone where growth and stress are in balance. This work, therefore, identifies where mixed forests are likely to succeed and where the effect may fade or reverse. By clarifying these ecological limits, our results offer a basis for decisions on forest restoration and plantation planning under a warming climate, and provide directions for carbon storage, wood production, and long-term soil fertility in regions where mixed planting is planned or already expanding.

Limitations and implications for future research

This global meta-analysis demonstrates that species mixing consistently enhances plant biomass accumulation and nutrient cycling in forest plantations, yet several limitations must be acknowledged. Most studies included in our synthesis were short to medium term (no more than 35 years), which highlights an important gap in understanding how diversity effects unfold over longer ecological timescales and across different successional phases. Additionally, while our dataset spans a broad geographic range, arid zones and high-latitude regions remain underrepresented in the literature, so our ability to evaluate context dependency in these environments is necessarily limited. Recognizing this data limitation, we emphasize that incorporating evidence from currently underrepresented climatic and biogeographic contexts could

refine estimates of effect sizes and potentially reveal new mechanisms driving diversity–function relationships. A deeper mechanistic understanding of species mixing is also needed, particularly regarding how species interactions influence belowground processes, such as litterfall decomposition, root exudation, and microbial functional traits, at a global scale. To enhance the applicability of our findings, we recommend that practitioners consider mixed-species plantations that pair functionally complementary species, a strategy supported by the robust positive effects identified in our synthesis. Future research would benefit from coordinated long-term studies that integrate biodiversity manipulations with biogeochemical monitoring and trait-based frameworks, which could help illuminate how missing data from underrepresented regions might reshape current interpretations of biodiversity effects. Such efforts will be essential for developing more context-aware guidelines for the design and management of planted forests that support biomass production and nutrient cycling.

Conclusions

This study demonstrates that mixed-species plantations enhance ecological functioning in ways not consistently achieved by monocultures. The concurrent increases in biomass and nutrient pools across stand strata indicate that species mixing improves the capacity of plantations to capture, retain, and recirculate resources rather than merely accumulating additional biomass. The coordinated amplification of crown development, belowground allocation, soil nutrient stocks, and microbial biomass suggests that higher compositional diversity promotes complementary resource acquisition and sustains internal nutrient cycling. The context dependence of these responses also shows that species richness alone is insufficient to guarantee superior functioning. The strongest effects occurred within specific climatic and structural ranges, implying that diversity benefits materialize when resource supply, stand development, and competitive intensity jointly support niche differentiation. Unimodal relationships with stand age, elevation, and stand density further indicate that diversity enhances functioning within finite physiological and environmental domains rather than universally. Together, these patterns show that species mixing increases the functional efficiency of plantations by strengthening the coupling between nutrient renewal and biomass formation. Where environmental and structural conditions align with complementarity, mixtures convert diversity into more effective carbon accumulation and nutrient retention. These findings provide a mechanistic foundation for incorporating species diversity in plantation design to sustain productivity and soil fertility over long-term development.

Materials and methods

Data collection

To evaluate the influence of species mixing on plant biomass accumulation and nutrient cycling in forest plantations worldwide, we conducted a comprehensive literature review of peer-reviewed studies. The search encompassed databases including China National Knowledge Infrastructure (CNKI), Google Scholar, and Web of Science, covering literature from January 1, 1990, to June 30, 2025 (Supplementary Fig. 1). We used the combination of the following keywords for the search: (species mixing OR mixed forest OR multispecies forest OR mixed plant* OR mix tree OR mixed cultivate* OR mixed cropping OR multispecies stands OR multispecies plant* OR polyculture plantation) AND (monoculture plantation OR single-species plantation OR pure forest OR pure stand).

All publications collected were screened based on the following criteria: (1) included only field studies on the impact of species mixing on biomass accumulation and nutrient cycling in forest plantations; (2) species mixing (treatment) and monoculture (control) plantations were established under the same site conditions; (3) monoculture and species mixing plantations were established simultaneously, and the overall tree planting density difference was less than 20%; (4) the means, corresponding standard deviations (s.d.) or standard errors (s.e.), and sample sizes for the control and treatment groups were provided or can be calculated. If a publication reported multiple experiments conducted in different locations, each observation was

considered an independent case. For studies that met the inclusion criteria, we extracted data on biomass (trees, shrubs, herbs, and litterfall) and nutrient indicators (soil, litterfall, and leaves) from the control and treatment groups from main texts, tables, and supplementary materials. For each indicator, the mean, standard deviation, and sample size were recorded. The data presented in the figures were digitized using the GetData software (version 2.26; GetData Pty Ltd, Moscow, Russia; <http://www.getdata-graph-digitizer.com/>).

To comprehensively evaluate the impact of mixed forests on plant biomass and nutrient cycling, we obtained stand age, stand density, species number (number of tree species in mixed forests) and crop rotation (number of crop rotations in monoculture artificial forests before planting to mixed forests), plant biomass (including trees, shrubs, herbs, understory vegetation and litterfall), commonly used soil physicochemical properties (including TC, SOC, SCS, MBC, TOC, TN, AN, MBN, TP, AP, MBP, C:N, C:P, and MBC:MBN), and nutrient content of leaf and litterfall from selected publications. We also extracted geographic variables (coordinates and altitude) and climate variables (MAT and MAP) for mixed-species plantations, and forest types (conifer-broadleaf mixed forest, conifer-conifer mixed forest, broadleaf-broadleaf mixed forest, and broadleaf-conifer mixed forest) of the mixed-species plantations. We recorded the species names as well as leaf size categories (coniferous or broadleaved) and leaf lifespan (evergreen or deciduous) for all monoculture and mixed species plantations in the screened data. In addition, we grouped the species mixing plantations based on the presence or absence of legumes in the mixed tree species. Ultimately, our dataset integrated 8450 paired observations from 328 peer-reviewed publications, covering the global plantation ecosystems (see Fig. 1 and Supplementary Data 1–2).

Statistics and reproducibility

To quantify species mixing effects on plantation biomass accumulation and nutrient cycling, we employed the natural log-transformed response ratio (RR) as our effect size metric⁴⁶. The calculation of RR was performed as follows:

$$RR = \ln \left(\frac{\bar{X}_t}{\bar{X}_c} \right) \quad (1)$$

where \bar{X}_t and \bar{X}_c represent mean values from mixed-species plantations (treatment) and monoculture plantations (control), respectively. The corresponding variance (v) of RR was calculated as follows:

$$v = \frac{S_t^2}{N_t \bar{X}_t^2} + \frac{S_c^2}{N_c \bar{X}_c^2} \quad (2)$$

where S_t and S_c are the s.d. values for the treatment and control groups, with N_t and N_c indicate their corresponding sample sizes.

The weighting factor of each response ratio was calculated as follows:

$$w = \frac{1}{v + \tau^2} \quad (3)$$

where τ^2 is the shared between-study variance across all studies. The formula for calculating τ^2 is as follows:

$$\tau^2 = \frac{\sum_{i=1}^m w_i (RR_i - \overline{RR})^2 - (m - 1)}{\sum_{i=1}^m w_i - \sum_{i=1}^m \frac{w_i^2}{w_i}} \quad (4)$$

where m ($i = 1, 2, \dots, m$) indicates the count of experimental replicates per group, and w_i is the weight of the i th experiment in the group.

To calculate the weighted overall effects (\overline{RR}), the following method was employed:

$$\overline{RR} = \frac{\sum_{i=1}^m w_i \times (RR_i)}{\sum_{i=1}^m w_i} \quad (5)$$

The percent change in plant biomass and nutrient content affected by species mixing was calculated as:

$$\text{Percentage}(\%) = 100 \times [(\bar{X}_c - \bar{X}_t) / \bar{X}_c] \quad (6)$$

To assess species mixing effects on plantation biomass accumulation and nutrient cycling, we applied a multilevel mixed-effects meta-analysis containing the ‘rma.mv’ function in the ‘metafor’ package (version 4.8-0)⁴⁷. Study ID was included as a random effect in all effect size estimations to address between-study heterogeneity. Treatment effects were considered significant if the 95% confidence interval (CI) of the treatment effect did not include zero ($P < 0.05$)⁴⁸. We employed Cochran’s Q -test to assess effect size heterogeneity, testing if observed variation exceeded random expectations⁴⁹. Our meta-analysis confirmed substantial residual heterogeneity in species mixing impacts on plantation biomass ($Q_t = 224,881.2$, $P < 0.0001$) and nutrient cycling ($Q_t = 777,980.3$, $P < 0.0001$), which we attempted to explain using various regulatory factors (Supplementary Table 6).

We conducted a single mixed effects meta regression to investigate how the impact of species mixing on plant biomass and nutrient cycling in global forest plantations is moderated by geographic location (latitude and elevation), climatic conditions (MAT and MAP), stand age and density, and the number of tree species in the mix. The Q -statistic (Q_m) of explanatory heterogeneity was used to test whether these moderators significantly affect the species mixing effects of biomass and nutrient cycling in forest plantations. A Q_m value of $P < 0.05$ indicates that moderators largely explain the heterogeneity of observed effect sizes⁵⁰.

To assess potential publication bias in our results, we employed funnel plots along with Egger’s test⁵¹ and Rosenberg’s fail-safe numbers⁵², which collectively provide robust evaluation of outcome robustness. The species mixing data exhibited a symmetrical funnel plot (Supplementary Fig. 2), and the Egger’s test results were not significant (plant biomass dataset: $z = 2.71$, $P = 0.007$; forest nutrient cycling dataset: $z = -1.67$, $P = 0.095$). Furthermore, we conducted a trim-and-fill analysis. This analysis imputed potentially missing studies, yet the adjusted overall effect estimate remained statistically significant, underscoring the robustness of our primary finding (Supplementary Fig. 3). Finally, Rosenberg’s fail-safe analysis showed that the significance levels of the plant biomass and forest nutrient cycling datasets were reduced to $P = 0.05$, respectively, requiring an additional zero-outcome study of 1.51×10^7 and 1.04×10^8 . Consequently, we do not believe publication bias influences the interpretation of study results⁵³. All analyses were performed using R v.4.5.1 software⁵⁴.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.30128551>.

Code availability

The code for the current analyses can be found at <https://doi.org/10.6084/m9.figshare.30128551>.

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Author contributions

H.Z. and J.G. conceived and designed this research; H.Z., H.F., and J.G. contributed to data analyses; H.Z. wrote the first draft of the manuscript, and edited by H.F., X.Q., M.Y., M. H., D. F.J., and J.G. All authors read and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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