

Meta-analysis reveals global variations in plant diversity effects on productivity

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Positive effects of plant diversity on productivity have been globally demonstrated and explained by two main effects: complementarity effects and selection effects^{1–4}. However, plant diversity experiments have shown substantial variation in these effects, with driving factors poorly understood^{4–6}. On the basis of a meta-analysis of 452 experiments across the globe, we show that productivity increases on average by 15.2% from monocultures to species mixtures with an average species richness of 2.6; net biodiversity effects are stronger in grassland and forest experiments and weaker in container, cropland and aquatic ecosystems. Of the net biodiversity effects, complementarity effects and selection effects contribute 65.6% and 34.4%, respectively. Complementarity effects increase with phylogenetic diversity, the mixing of nitrogen-fixing and non-nitrogen-fixing species and the functional diversity of leaf nitrogen contents, which indicate the key roles of niche partitioning, biotic feedback and abiotic facilitation in complementarity effects. More positive selection effects occur with higher species biomass inequality in their monocultures. Complementarity effects increase over time, whereas selection effects decrease over time, and they remain consistent across global variations in climates. Our results provide key insights into understanding global variations in plant diversity effects on productivity and underscore the importance of integrating both complementarity and selection effects into strategies for biodiversity conservation and ecological restoration.

In the past three decades, biodiversity–ecosystem functioning relationships (BEFs) have been the focus of ecological studies, showing increasing evidence that biodiversity improves ecosystem functioning, such as productivity^{2,5,7}. The net biodiversity effect (NE) can be further partitioned into the complementarity effect (CE; driven by niche partitioning, abiotic facilitation and biotic feedback) and the selection effect (SE; due to the over-proportional performance of highly productive species)^{1–4,8}. Previous studies have indicated that a wide range of factors, such as stand age and plant functional indices, may influence the magnitudes of BEFs and the components (CEs and SEs)^{4–6}. However, it remains poorly understood what mechanisms drive the varied outcomes in global BEF experiments with distinct diversity, ecosystem types, climates and stand age. An improved understanding of the processes and their conditional operation will help us to anticipate the consequence of context-dependent diversity loss on plants themselves and organisms of other trophic levels^{2,7,9}, and to develop strategies to cope with these changes.

There are several proposed mechanisms to explain the CEs. Plant functional and phylogenetic diversity are predicted to play key roles in the CEs (Fig. 1). As leaf functional traits indicate leaf economic spectrum and life-history strategies^{10,11}, functional diversity, which often increases with species richness, can indicate high niche partitioning^{12–14}. In particular, nitrogen (N) is usually limited in global terrestrial ecosystems, and N-fixing plants increase the availability of resources for

non-N-fixing neighbours^{15,16}. As such, plant mixtures with both N-fixing and non-N-fixing plants may show more positive CEs because of the facilitative effects of N-fixing plants on non-N-fixing neighbours. As evolutionarily closely related species tend to have similar functional traits¹⁷, phylogenetic diversity can also reflect niche partitioning. Additionally, phylogenetic diversity may promote positive biotic feedback with increasing community resistance to host-specific insect or pathogen attacks^{18,19}.

Positive SEs rely on the over-proportional performance of some productive species^{1,20}, which have higher intrinsic growth rates and competitive advantage over lower-performance species^{21,22}. The productivity of a constituent species in its monoculture can, to some extent, reflect the species fitness to the local environment; mixing species with high fitness differences allows those with higher productivity to obtain a disproportionate share of resources to support their over-proportional performance^{21–23}, which thus promotes positive SEs. As such, we expected that higher species biomass inequality in their monocultures (hereafter ‘inequality’) would lead to greater positive SEs in mixtures. Alternatively, previous studies have attributed SEs to the key role of dominant species with their functional properties in influencing ecosystem processes^{3,24,25}. Accordingly, in plant mixtures, high community-weighted means (CWMs) of functional traits that are associated with high growth rates, such as leaf N content, would be expected to have stronger SEs^{3,26,27} (Fig. 1).

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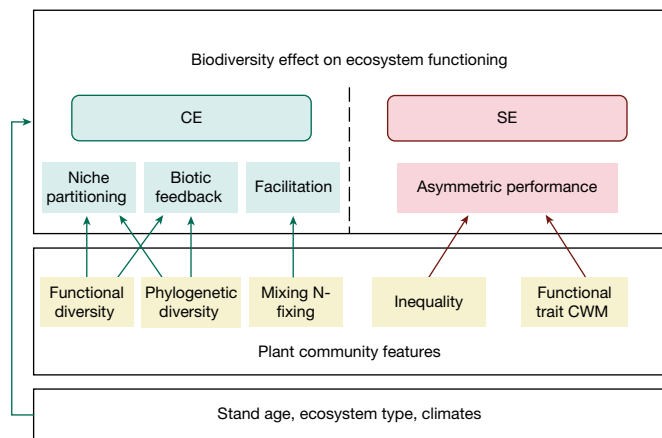


Fig. 1 | Conceptual diagram showing the hypothesized factors for the CE and SE in global plant diversity experiments. Mixing N-fixing refers to mixing of N-fixing and non-N-fixing species; inequality indicates species biomass inequality of the monocultures; functional trait CWM is the community-weighted mean of the functional traits of plant mixtures.

The NE and its components may vary with stand age, ecosystem types and climate. Older stands can allow temporal partition of resource use²⁸ and improve partitioning in aboveground space and soil resources²⁹, thus increasing CEs^{8,30}, whereas SEs remain similar or decrease as the relative abundance of fast-growing, early successional species declines^{3,5,31}. Furthermore, NEs and CEs may be less pronounced in containers than in the field, such as forests and grasslands, for which there could be more heterogeneous microenvironments that allow niche partitioning⁸. Also, as positive species interactions tend to increase with higher environmental stress³², drier and colder forests have shown more pronounced positive diversity effects³³. Alternatively, the positive effects of diversity can be greater in an environment favourable to growth as a result of more resources (niches) available for partitioning²⁵.

By compiling a dataset with 4,598 observations of plant mixtures (each paired with the monocultures of all constituent species) from 452 studies of plant mixture and diversity experiments in different ecosystems (Extended Data Fig. 1), we conducted a meta-analysis to show the variations in NE, CE and SE among studies by examining the roles of species richness, functional and phylogenetic diversity, CWMs of functional traits, the mixing of N-fixing and non-N-fixing species in plant mixtures and inequality, as well as stand age and climatic factors including mean annual temperature (MAT) and aridity index. As individual studies report biomass with different measurement methods and units, here we investigated the 'relative' NE, CE and SE with their values divided by "the weighted (by the initial relative abundance of species in the mixture) average of the monoculture yields for the constituent species"; that is, the expected yield of the mixture¹. To cover a wide range of variation in diversity effects, the dataset included as many plant mixtures as available, even those mixed by closely related species from the same genus, and various systems, including grasslands, forests, wetlands, croplands, containers and aquatic systems. For functional traits, here we focused on leaf N content per unit of dry mass (leaf N) and specific leaf area (SLA), which are among the most important traits reflecting plant economic spectrum and the most available traits from the global database (TRY plant trait database)^{10,34}.

Average diversity effects

Species richness in plant mixtures in our dataset was on average 2.6, spanning from 2 to 18. The 'relative' NE, was on average 0.152 (95% confidence interval (CI) based on a meta-regression model, CI: 0.128–0.177) (Fig. 2a); that is, the species mixtures yielded 15.2% higher productivity than the expected yield based on corresponding monocultures across

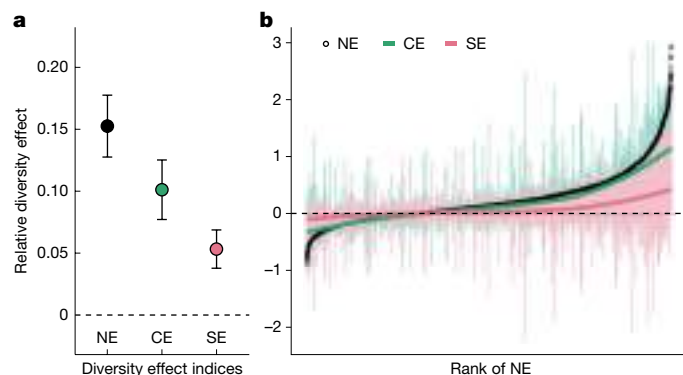


Fig. 2 | The overall performance of CE and SE across the dataset. **a**, The mean relative NE, CE and SE with 95% CIs across the dataset based on the entire dataset in global plant mixture experiments ($n = 4,598$). **b**, The variation of CE and SE along the rank of NE. Curves were fitted with locally estimated scatterplot smoothing.

the global collection of plant mixture and diversity experiments. Yet, about 70% of NE observations were positive and 30% were negative (Supplementary Table 1). Across all observations, the 'relative' CE and SE were on average 0.101 (CI: 0.077–0.125) and 0.053 (CI: 0.038–0.069), respectively (Fig. 2a). As NE varied, CE demonstrated a greater range of fluctuation compared to SE, with more positive and more negative CE than SE at the highest and the lowest values of NE, respectively (Fig. 2b). Furthermore, the difference between relative CE and relative SE effects (CE – SE) was on average higher than 0 (mean: 0.053; CI: 0.023–0.083), indicating overall more positive CE than SE.

Our finding provides global-scale evidence that NE, CE and SE were overall positive across various plant mixtures and ecosystems. This result substantiates the long-held hypothesis that CEs and positive SEs jointly contribute to positive BEF¹, complementing previous studies with some emphasizing CEs^{5,31} whereas others highlight SEs²⁰. It is worth noting that about 30% of observations showed a negative NE, because our dataset spanned as varied plant species mixtures as possible, including those with species from the same genus, rather than only from the BEF studies focusing on positive diversity effects (detailed data selection criteria in Methods). Also, our results indicate that the variation of NEs is more dependent on the CE than the SE. The upper limit of CEs was greater than that of SEs. Strong CEs can sometimes lead to transgressive overyielding^{3,31}; that is, mixtures performed better than even the best monoculture. Moreover, building on previous findings that explored the variation of CEs and SEs along species richness and stand age^{4,5,31}, our study provides evidence that CEs are associated with niche partitioning, abiotic facilitation and biotic feedback, whereas SEs result from the asymmetry of species performance in productivity across diverse plant species assemblages.

Variations in diversity effects

Our mixed-effect meta-regression models revealed several important mediators for CE and SE across the global mixture and diversity experiments (the number of paired observations of plant mixtures and monocultures, $n = 4,598$) (Fig. 3). CE increased strongly with species richness and phylogenetic diversity (meta-regression coefficient, $r = 0.065$ and 0.069 , respectively) (Fig. 3a,c and Supplementary Table 2), whereas SE showed an increase with species richness and non-significant variation with phylogenetic diversity ($r = 0.017$ and -0.001 , respectively) (Fig. 3b,d). The mixing of N-fixing and non-N-fixing species exerted a stronger positive CE than those without mixing (increased by 0.183), but a non-significant effect on SE (Fig. 3e,f). Also, both CE and SE increased with higher inequality ($r = 0.031$ and 0.056 , respectively) (Fig. 3g,h). As the sum of CE and SE, NE increased significantly with species richness,

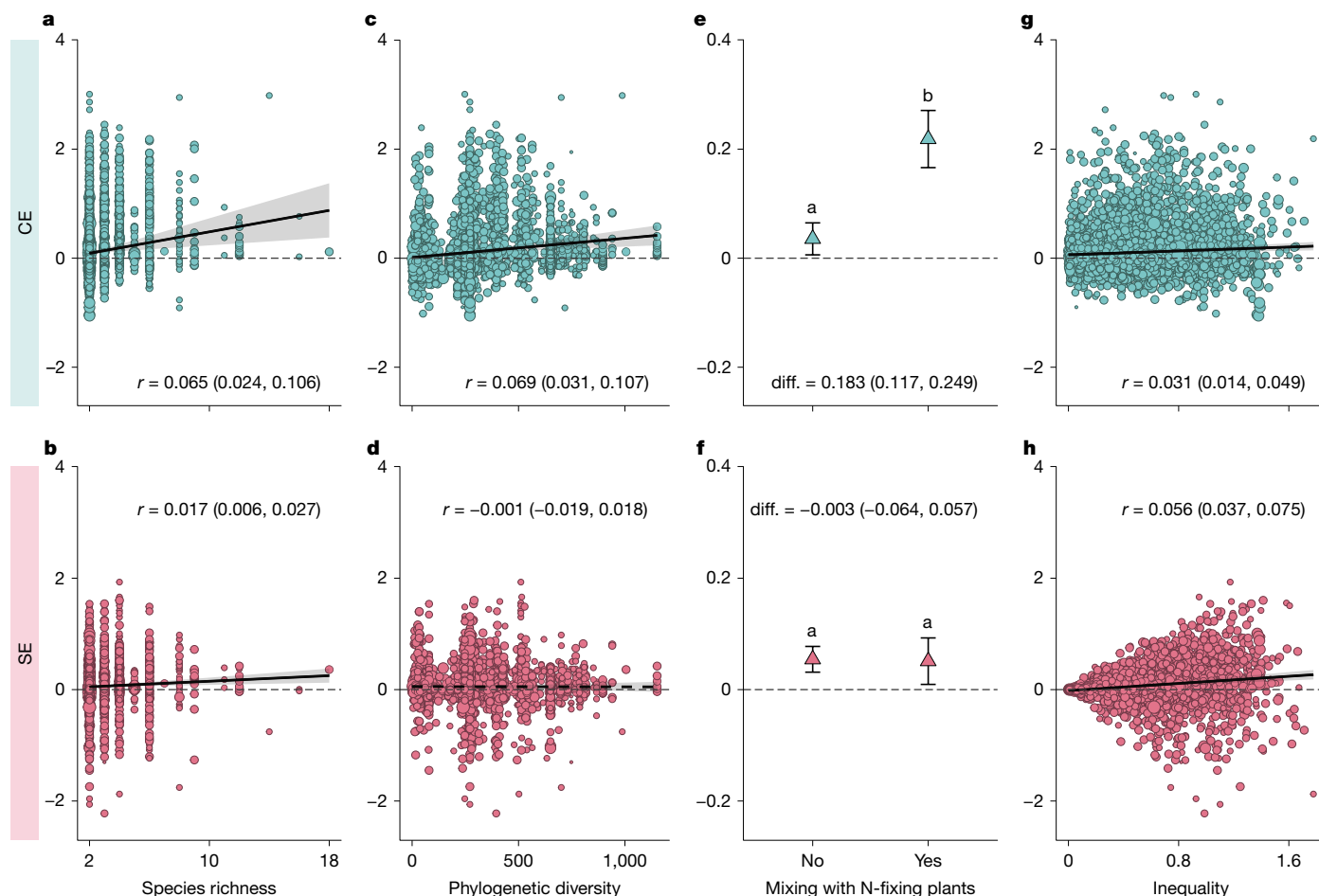


Fig. 3 | Bivariate relationships of relative CE and relative SE with different plant community characteristics. Variation of relative CE and relative SE with species richness (**a,b**), phylogenetic diversity (**c,d**), mixing with N-fixing plants (**e,f**), and inequality (**g,h**). Inequality indicates species biomass inequality, measured as coefficient of variation, of monoculture biomass. The relationships are evaluated using two-sided *t*-tests in mixed-effect meta-regression models followed by robust variance estimation (RVE), based on the entire dataset of

plant mixture observations ($n = 4,598$). In **a–d** and **g,h**, the regression line represents the response to a predictor with the 95% CI shaded, and the values of the estimated coefficient and 95% CI are shown in each subplot; circle sizes are proportional to the relative weights of the observations. In **e,f**, the mean CE or SE and 95% CI are shown for mixing and not mixing with N-fixing plants (1,934 and 2,664 observations, respectively), and significant difference ($P < 0.05$) is marked as different letters; diff., the difference in means (95% CI).

phylogenetic diversity, mixing with N-fixing plants and inequality; CE – SE increased with higher species richness, phylogenetic diversity and mixing with N-fixing plants (Extended Data Fig. 2).

To further investigate whether inequality promotes positive SEs irrespective of their inherent mathematical relationship, we developed a ‘modified’ SE that excluded the mathematical influence of the absolute differences between species biomass in monocultures (Extended Data Fig. 3) (Methods). The result showed that the modified SE still increased with inequality ($r = 0.045$, CI: 0.020–0.070) (Extended Data Fig. 4 and Supplementary Table 2), indicating that inequality promoted SEs irrespective of their inherent mathematical relationship.

On the basis of the dataset with available leaf N data ($n = 2,273$), we found that CE was more positive with increasing functional diversity (measured as Rao’s quadratic entropy, Q) of leaf N content and CWM of leaf N content of plant mixtures ($r = 0.065$ and 0.054 , respectively) (Fig. 4a,b and Supplementary Table 2). Meanwhile, with varied functional diversity or the CWM of leaf N, SE showed non-significant variation and NE showed similar trends with CE (Fig. 4c,d and Extended Data Fig. 5). In addition, higher functional diversity and CWM of leaf N were associated with the mixing of N-fixing and non-N-fixing species (Fig. 4). Without the mixing of species that fix N and those that do not fix N, the relationships between CE with functional diversity and CWM of leaf N became weaker ($r = 0.040$, CI: 0.009–0.070) and non-significant

($r = -0.006$, CI: -0.039 – 0.027), respectively (Extended Data Fig. 6). The functional diversity and CWM of SLA showed non-significant relationships with CE, SE or NE, based on the dataset with available SLA ($n = 2,784$) (Extended Data Fig. 7).

Our results provide global-scale evidence that the CE was more positive with greater species richness and phylogenetic diversity across plant diversity experiments. These results are consistent with the expectation that phylogenetic diversity reflects the high-dimensional diversity of plant functional characteristics and niche differentiation, which enhances CEs^{14,35,36}. This result may further indicate the role of positive biotic feedback in promoting CEs, with higher phylogenetic diversity reducing the susceptibility of plant communities to species-specific pathogens and herbivores^{18,37}. Furthermore, our results showed that plant mixtures with N-fixing and non-N-fixing species exerted stronger positive CEs than those without, which is in line with the widely recognized role of facilitation in BEFs, particularly improved soil N availability by N-fixing plants^{8,38}. It should be noted that the plant mixtures without mixing of N-fixing and non-N-fixing species still showed an overall positive CE (Fig. 3e), indicating that positive CEs rely on several different mechanisms rather than only on the facilitation of N-fixing plants^{8,39}.

Moreover, our results showed that the functional diversity of leaf N was also an important factor in promoting CEs, whereas that of SLA was not. These results indicate that, although the diversity of functional

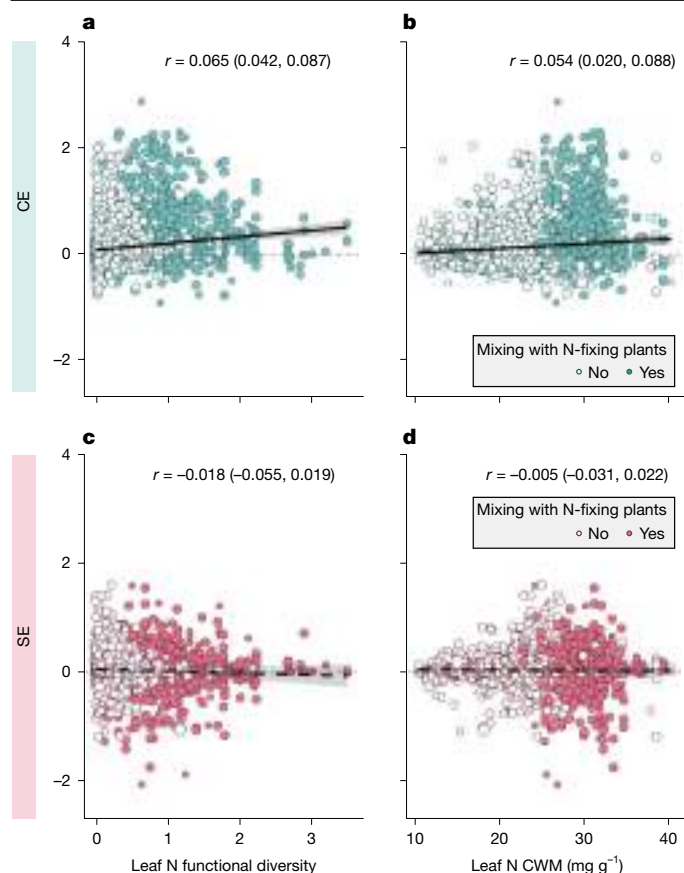


Fig. 4 | Bivariate relationships of the relative CE and relative SE with the functional diversity (Rao's Q) and CWM of leaf N content. Variation of relative CE (a,b) and relative SE (c,d) along leaf N functional diversity and leaf N CWM. The relationships are evaluated using two-sided t -tests in mixed-effect meta-regression models followed by RVE, based on the plant mixture observations with leaf N content ($n = 2,273$). The regression line represents the response to a predictor with the 95% CI shaded, and the values of the estimated coefficient and 95% CI are shown in each subplot. Observations with the mixing of N-fixing and non-N-fixing species were highlighted as darker colours. The sizes of the circles are proportional to the relative weights of the observations.

traits can reflect niche partitioning among species^{10,11}, whether it plays a key role in promoting CEs and biodiversity effects may depend on the specific function or niche that the trait can reflect. Together with previous studies^{40,41}, our results indicate that the leaf nutrient content may be more directly involved in changes in ecosystem functions to varying biodiversity than a leaf morphological trait. As leaf N variation reflects fast- versus slow-growing species with different nutrient use strategies^{10,34}, our results indicate the role of complementarity of nutrient resource use in positive BEFs. Moreover, we showed that the relationship between CEs and the functional diversity of leaf N content was greater with the mixing of N-fixing and non-N-fixing species, indicating that the functional diversity of leaf N reflects not only the niche partitioning of N use between species, but also the facilitation effect of N-fixing plants, both of which contribute to positive CEs^{7,8,38}.

Our results showed that inequality was the key factor for either the SE or the modified SE, which excluded the inherent mathematical connection with the difference in species biomass in monocultures. This result indicates that positive SEs can, to some extent, be predicted by the difference in species biomass of their monocultures, as highly productive species could exploit a disproportionate share of resources and benefit more from mixing than do other species²³. This result may also indicate that fitness differences between species contribute to enhancing positive effects of plant diversity, as long as the niche differences between

species help maintain their coexistence in the mixture. Meanwhile, we showed that higher inequality also promoted CEs. This result is consistent with the expectation that differences in plant sizes, heights and crowns promote CEs as a result of niche differentiation^{42,43}.

Furthermore, we showed that the SEs did not change with the CWM of leaf N or SLA of plant mixtures, weighted either by initial planting proportions or realized biomass proportions at the biomass measurement (Supplementary Table 3). Although the absolute productivity of plant mixtures with high-productivity species can be higher than those with low-productivity species⁴⁴, their productivity relative to their respective means of monocultures may not differ if the SE does not occur among constituent species. Although CWMs of plant functional properties in mixtures can be associated with the dominance of high-productivity species and average productivity of the mixtures²⁷, our results indicate that CWMs do not necessarily influence SEs. Instead, positive SEs rely on the asymmetry of species fitness or performance, as indicated by the empirical evidence in this study. However, we cannot rule out the possibility that the CWMs of some other functional traits in mixtures rather than leaf N and SLA are more connected to the SEs.

Dependency on stand age and ecosystems

Furthermore, by conducting mixed-effect meta-regression models, we showed that CE turned more positive, whereas SE tended to be less positive, with increasing stand age ($r = 0.071$ and -0.024 , respectively) (Fig. 5a,b and Supplementary Table 2). CE was also significantly different among ecosystem types, with significantly more positive effects in grassland (fixed-effect estimate: 0.211; CI: 0.138–0.284) and forest (0.203; CI: 0.161–0.246) than in cropland (0.042; CI: -0.022 –0.107), wetland (-0.052 ; CI: -0.104 –0.001), container (0.050; CI: 0.020–0.080) and aquatic systems (0.011; CI: -0.132 –0.154) (Fig. 5c). On the contrary, SE was stronger in the container (0.072; CI: 0.047–0.097) than in the forest (0.019; CI: -0.007 –0.046) and wetland (0.007; CI: -0.001 –0.015) (Fig. 5d). Also, CE was more positive among woody plants than among herbaceous plants, whereas SE was slightly stronger between herbaceous plants than among woody plants (Fig. 5e,f). We also examined the effects of different moderators on CE and SE while accounting for other factors by fitting them into one model, and the results were qualitatively consistent with the results examined individually (Supplementary Table 4).

NE increased significantly with stand age and was stronger in grassland (0.263; CI: 0.188–0.338) and forest (0.217; CI: 0.179–0.255) and weaker in container (0.121; CI: 0.087–0.155), cropland (0.096; CI: 0.030–0.162) and aquatic ecosystems (0.033; CI: -0.098 –0.165) (Extended Data Fig. 2). Similarly, CE – SE increased with stand age and was greater in grassland and forest than in cropland, wetland and container, and greater in woody plant mixtures than in herbaceous plant mixtures (Extended Data Fig. 2). We also analysed the experiments carried out in the field to assess whether the background climate influences the effects of biodiversity ($n = 3,091$). The analyses showed that CE, SE and NE did not vary significantly along MAT or aridity index (Extended Data Fig. 8).

Consistent with previous experimental evidence^{3,5,31}, our results indicate that CEs increase over time in species-diverse communities, which can be explained by different mechanisms. For example, in ecosystems dominated by perennial species such as trees, species differences in growth strategies become greater with age, allowing for higher niche partitioning in the community¹³; for annual plants, living history in high-diversity communities alters offspring genes and functional traits, which can promote CEs across generations⁴⁵. It should be noted that CE exhibits a logarithmic growth pattern with age, indicating that CE increases with age at a decreasing rate. This finding partially agrees with a previous synthesis showing an initial increase and then a decrease in CEs in tree mixtures with stand age⁴. However, in both studies, the fewer observations from older stands may restrict the ability to make

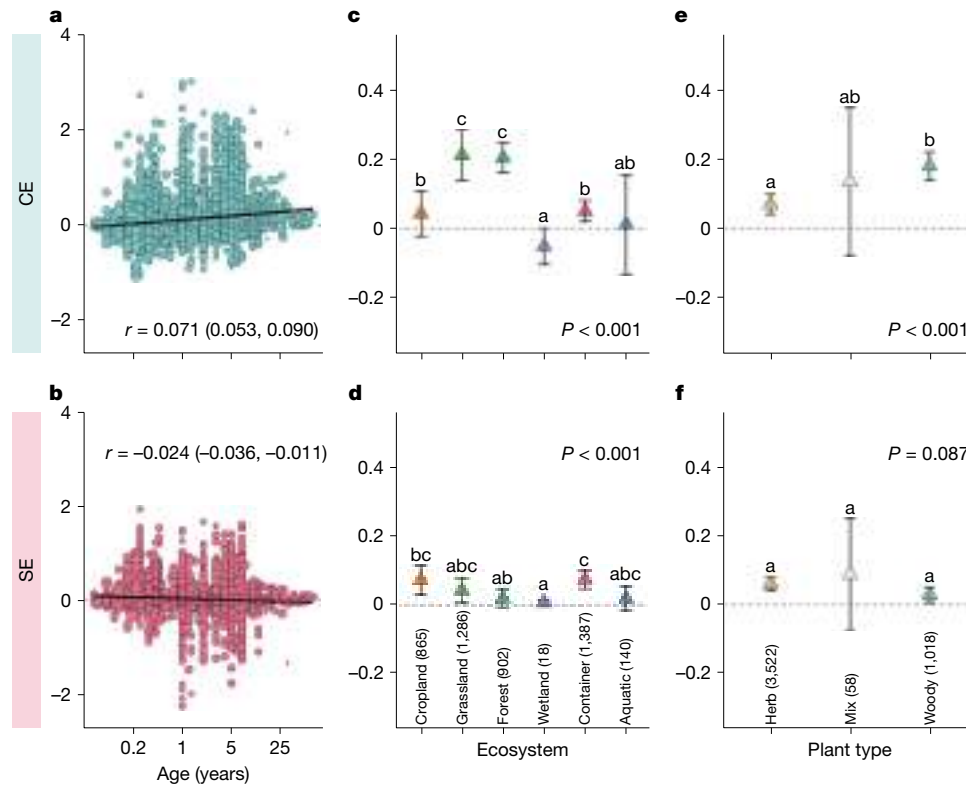


Fig. 5 | Bivariate relationships of relative CE and relative SE with stand age, ecosystem and plant type. Variation of relative CE and relative SE with age (a,b), ecosystem type (c,d), and plant type (e,f). The relationships are evaluated using two-sided *t*-tests in mixed-effects meta-regression models followed by RVE, based on the entire dataset of plant mixture observations ($n = 4,598$). In a and b, the regression line represents the response to a predictor with the 95% CI shaded, and the values of the estimated coefficient and 95% CI are shown in each subplot; circle sizes are proportional to the relative weights of the

observations. In c–f, the mean CE or SE and 95% CI are shown for different ecosystems and plant types with the number of observations shown in brackets; the *P* values of the multiple comparisons are adjusted with Benjamini–Hochberg procedure, with significant differences ($P < 0.05$) marked as different letters; in c–e, the exact *P* values are 7.0×10^{-14} , 1.0×10^{-5} and 8.5×10^{-5} , respectively. In e and f, the plant mixtures are classified into herbaceous plants, woody plants and mixtures of both herbaceous and woody plants.

long-term predictions about CEs. We recommend that future research deepens our knowledge of CEs with more observational evidence in old mixed stands. Moreover, reduced SEs with age indicate that the advantages of high-productivity species decrease in the long term³. Our results that NE relies more on CE than SE, and that NE also increases with stand age, indicate an increasingly deepened negative impact of biodiversity loss on ecosystem functioning over time^{5,31}.

Our results also showed significantly stronger positive CEs in grassland and forest than in cropland, wetland, containers and aquatic systems. These results indicate that the highly manipulated and homogeneous environment in cropland and containers may be less favourable for niche partitioning. The lower CEs in aquatic systems may also indicate that the interspecific competition of aquatic plants is not always lower than their intraspecific competition⁴⁶. In addition, we showed that the SE was greater in containers than in forests and wetlands. The shorter durations of experiments in containers might have contributed to the weaker CEs and stronger SEs.

Caveats and conclusions

The BEFs summarized from manipulated plant diversity experiments may not fully mirror those in natural ecosystems, which have some distinct characteristics, such as different species compositions and more heterogeneous environments⁴⁷. However, our analysis based on manipulated experiments provides useful insights for BEF studies in natural ecosystems^{26,27,48}: the functional diversity of certain functional traits, specifically leaf N content, is quantitatively evidenced as

a measure of CEs; caution should be taken to interpret CWMs of some functional traits (at least leaf N content and SLA) as the surrogate of SEs. Furthermore, given the expansion of planted forests and global efforts of ecosystem restoration^{14,49}, our results may provide insight for restoration practices to promote biodiversity and ecosystem functions at the same time. It should also be noted that this study is based on the synthesis of past experimental results with imbalanced sampling efforts and different experimental conditions in different ecosystems. As such, caution should be taken to interpret the mean diversity effects between ecosystem types.

Overall, our analysis offers global-scale evidence that CEs increase with species richness, phylogenetic diversity, the mixing of N-fixing and non-N-fixing species, inequality, functional diversity of leaf N and stand age. Furthermore, we found inequality to be a vital indicator of SEs, clarifying the cause of SEs as the difference in species performances rather than the community averages. The varied CEs and SEs among ecosystems indicate that it may be necessary to separately consider the different components of biodiversity effects for biodiversity conservation and restoration in different ecosystems.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-024-08407-8>.

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Methods

Data collection

We followed the guidelines of PRISMA (preferred reporting items for systematic reviews and meta-analyses)^{50,51} to build up the dataset for NE, CE and SE in manipulated plant mixture and diversity experiments (Extended Data Fig. 1a and Supplementary Table 5). Specifically, we first searched for all peer-reviewed journal articles and theses for related studies using the Web of Science (core collection; <http://www.webof-knowledge.com>), Google Scholar (<http://scholar.google.com>) and the China National Knowledge Infrastructure (<https://www.cnki.net>) until 1 December 2023. We used different combinations of keywords, including (species diversity OR species richness OR plant mixture OR plant diversity OR tree mixture OR mixed plantation OR pure and mixed) AND (biomass OR growth OR productivity OR basal area OR overyielding OR complementarity effect OR selection effect OR sampling effect OR competition). Additionally, we investigated all studies that cited ref. 52, whose replacement series design is widely used in plant mixture or diversity manipulation experiments. We also examined the datasets of previous syntheses and meta-analyses with related topics as supplementary data sources (Supplementary Table 6).

To ensure the quality of the dataset, we established several criteria to determine whether each study can be included in our dataset, as follows. (1) The effects of plant diversity or mixture are isolated from other factors or treatments. (2) The planting densities of plant mixtures and monocultures were constant following the substitutive design. For example, if a species was planted as 120 individuals per square metre in its monoculture, it should be planted as 40 individuals per species per square metre in a 1:1:1 three-species mixture. (3) No barrier was established between plant individuals in mixtures or monocultures. (4) Biomass data for each species in mixtures and corresponding monocultures are available in text, tables or figures. (5) Data were recorded only once if they were repeatedly reported in several articles. To investigate as many species combinations as possible, we included not only studies focusing on BEFs but also studies examining interspecific competition or interactions, even between species of the same genus, as long as their experimental designs fell in our data selection criteria as above. Two of the three authors independently followed the PRISMA guidelines, searched by the different combinations of keywords, and examined each related literature against the data selection criteria. The two authors examined 37 studies that were only selected by one of the authors more carefully and interactively to determine their inclusion following the data selection criteria. All unselected literature was listed with the reasons for exclusion (Supplementary Table 7).

In total, we obtained 452 studies with paired observations of biomass of all species in plant mixtures and corresponding monocultures across different ecosystem types, including grasslands (60 studies), forests (112 studies), wetlands (3 studies), croplands (42 studies), containers (213 studies) and aquatic systems (25 studies)⁵³ (Extended Data Fig. 1 and Supplementary Table 8); and plant types, including woody plants, herbaceous plants and mixtures with both woody and herbaceous plants. We used Plot Digitizer v.2.0 (Department of Physics, University of South Alabama) to digitally extract the data reported in graphs.

We obtained plant biomass, species identity, species richness, species proportion, stand age, geographical location (latitude and longitude), ecosystem type, plant type and climate for each observation (Extended Data Fig. 9 and Supplementary Table 9). The biomass of each species in mixtures and monocultures was recorded or calculated as the mean value of replicates. We included several studies that reported annual biomass productivity (or growth rate) of trees, which is strongly and positively related to their biomass at a young age⁵⁴. The biomass was estimated as the total or aboveground biomass or productivity, the carbon stock of the trees, the volume of wood or the basal area in the original studies. The biomass measured for individuals was converted to area-based with the density of the species in individual plots. The

proportions of species in the plant mixtures were recorded on the basis of their respective seedling or seed counts. Plant mixtures with non-N-fixing plants and N-fixing plants, including Fabaceae species and N-fixing actinorhizal plants¹⁵, were marked as the mixing of N-fixing and non-N-fixing species. Inequality was calculated as the coefficient of variation of species biomass of their corresponding monocultures. Stand age referred to the years between the establishment of the stand or the beginning of the experiment and the measurement of biomass. For field experiments, the MAT was recorded from the literature if available; otherwise, it was derived from the WorldClim v.2.1 dataset⁵⁵. To indicate the climatic water condition of each experimental location, we derived the aridity index (the ratio of the mean annual precipitation to the mean annual potential evapotranspiration) from the WorldClim dataset⁵⁵.

Phylogenetic and functional indices

Before the construction of the phylogenetic tree, we normalized the scientific names of all plant species and obtained their genus and family names using the taxize package⁵⁶, which was based on the database of the National Center for Biotechnology Information. Then we built the phylogenetic tree for all species using the V.PhyloMaker package⁵⁷, which was based on GenBank taxa with a backbone provided by Open Tree of Life⁵⁸. Subsequently, we calculated phylogenetic diversity as Faith's index⁵⁹, which is the sum of the branch length of all species and is commonly used as the index for phylogenetic diversity^{60,61}.

As plant functional traits vary in data availability among species³⁴, investigating several functional traits at the same time may cause a substantial reduction in the dataset. As such, here we focused on the functional trait of leaf N content per unit of dry mass (leaf N) and SLA, which are among the most important and widely used plant biochemical and morphological traits and reflect plant economic spectrum^{10,34}. We derived the leaf N and SLA data for each species from the TRY plant trait database³⁴. The functional properties of the plant mixtures, including the functional diversity and the CWM, were calculated separately for leaf N and SLA for the plant mixtures with the trait data available for all included species. The functional diversity was calculated as Rao's *Q* (refs. 62,63) and the CWM was calculated as the weighted mean of leaf N and SLA using the FD package⁶⁴, based on the species trait data and the species planting proportion in the mixtures. Using the species planting proportion has the advantage of providing insights into predicting the outcomes of CEs and SEs on the basis of known species information at the beginning or ahead of stand establishment, which allows experimental, cropping or restoration designers to assemble species on the basis of a priori rules¹³. We also calculated Rao's *Q* and CWM of LN and SLA on the basis of the realized species biomass proportion at the time of biomass measurement, which showed similar positive variation of CE along the Rao's *Q* and CWM of LN, and also showed decreased SE along the Rao's *Q* of LN and SLA (Supplementary Table 3).

Diversity effect

The quantification of the CE and SE was based on the partitioning of the NE as indicated by ref. 1:

$$NE = Y_O - Y_E = \sum_i \Delta RY_i M_i \quad (1)$$

$$CE = N \overline{\Delta RY} \overline{M} \quad (2)$$

$$SE = N \times \text{cov}(\Delta RY_i, M_i) = \sum_i ((\Delta RY_i - \overline{\Delta RY}) \times (M_i - \overline{M})) \quad (3)$$

where Y_O is the observed yield of plant mixture, calculated as the sum of the observed yield of each species in the mixture; Y_E is the expected yield of the plant mixture, calculated as the sum of the yield of corresponding plant monocultures multiplied by their seedling or planting

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proportion in mixtures; ΔRY_i is the difference between the ‘observed relative yield’ of species i in mixtures and the ‘expected relative yield’ (the proportion seeded or planted) of species i ; M_i is the yield of species i in monoculture; $\overline{\Delta RY}$ is the average of ΔRY_i of all species; \overline{M} is the average of M_i , that is, the average of all species in monoculture; N is the number of species in the mixture; and cov is the covariance. To be comparable among studies with different biomass measurement methods and units, we calculated the ‘relative’ NE, CE and SE by dividing them by the sum of the expected yield of all species corresponding to the mixture; that is, “the weighted (by the initial relative abundance of species in the mixture) average of the monoculture yields for the constituent species”⁷¹. As outliers are present in diversity manipulation experiments⁶⁵ and affect the validity of the conclusions from a meta-analysis⁶⁶, any NE, CE and SE with a standardized residual value exceeding the absolute value of three were removed as outliers⁶⁷. Our analyses showed that the overall diversity effects were not sensitive to the exclusion of the outliers, with the mean diversity indices remaining similar after removing outliers (Supplementary Table 10).

Also, as meta-analyses traditionally rely on the effect sizes to compare the outcomes of different studies⁶⁸, we also estimated the effect size for the plant mixture effect as the natural log-transformed response ratio (lnRR):

$$\ln RR = \ln \left(\frac{Y_o}{Y_e} \right) \quad (4)$$

where Y_o and Y_e are the observed and expected yields of plant mixture as explained above. The lnRR of the plant mixture effect is mathematically related to the relative NE.

Data analysis

We estimated the overall NE, CE and SE in the weighted, mixed-effect model using the `rma.mv` function in the R package `metafor`⁶⁹. We included the random effect of study ID to account for the between-study effects and quantify between-study heterogeneity, and we included the random effect of observation ID to account for the within-study effects and quantify within-study heterogeneity⁷⁰. The weight for each observation is usually calculated by the inverse of sampling variance when it was available⁶⁸. However, sampling variance data (s.e.m., s.d. or 95% CI) were only available in less than half of all studies in our dataset (185 of 452 studies). Also, as intensely controlled indoor experiments typically have lower sampling variances than field experiments, weighting by inverse variances would systematically assign higher weights to indoor experiments than to field experiments. An alternative weighting function was to calculate the weight of each observation (W_r)^{71,72}:

$$W_r = \frac{N_c \times N_t}{N_c + N_t} \quad (5)$$

where N_t and N_c are the numbers of replicated plots of plant mixtures and monocultures, respectively.

We examined the relationships between W_r and the sampling variance on the basis of the sub-dataset with reported sampling variances. The sampling variance for each species in the mixture and its monoculture (v_{ind}) was calculated on the basis of ref. 73:

$$v_{ind} = \frac{S_t^2}{N_t \times \overline{X}_t^2} + \frac{S_c^2}{N_c \times \overline{X}_c^2} \quad (6)$$

where S_t and S_c are the standard deviations of species biomass in the mixture and its monoculture, respectively; \overline{X}_t and \overline{X}_c are the mean biomass of the species in the mixture and monoculture, respectively. The sampling variance for a plant mixture, v_{mix} , was approximately indicated by the average v_{ind} of all constituent species. Parameter v_{mix} showed a significant positive relationship with $1/W_r$ based on the sub-dataset

with 2,298 observations that reported sampling variances ($F = 70.94$, $P < 2.2 \times 10^{-16}$). In this study, we used a sampling variance as ‘corrected $1/W_r$ ’, which was based on $1/W_r$ and corrected by the relationship between $1/W_r$ and v_{mix} . To validate this, we followed ref. 74 and used two different methods to simulate sampling variances for lnRR: the ‘all cases’ approach, in which the average coefficient of variation was used to estimate sampling variances for all observations and the ‘multiplicative’ approach, in which sampling variance is assumed to be proportional to W_r . We compared the overall lnRR derived from these two methods with corrected $1/W_r$ as sampling variance, and they showed similar results with each other (Supplementary Table 11), indicating that corrected $1/W_r$ is valid for sampling variance in this study. Moreover, we examined the heterogeneity of the diversity effect in our dataset using the I^2 statistic, which “describes the percentage of variability in the effect estimates that is due to heterogeneity rather than sampling error”⁷⁵. We found that between-study I^2 for the lnRR was 25.0% and that the within-study I^2 was 58.2%. The higher within-study heterogeneity indicates that different factors, including plant mixture characteristics and experimental ages, alter the plant diversity effects even in each study.

We examined the influence of potential predictors, including species richness, phylogenetic diversity, mixing with N-fixing species, inequality, stand age, ecosystem type and plant type on the variation of NE, CE and SE:

$$DE = \beta_0 + \beta_1 F + \pi_{studyID} + \pi_{obsID} + \varepsilon \quad (7)$$

where DE is the relative diversity effect, that is, one of NE, CE and SE; β is the coefficient to be estimated; F is the factor to be investigated; $\pi_{studyID}$ and π_{obsID} are the between-study and within-study random effects indicated by study ID and observation ID, respectively; and ε is sampling error. Meta-regression models were analysed with the `rma.mv` function. We further examined whether these factors remained robust while accounting for other factors by building a full model with different potential predictors:

$$DE = \beta_0 + \beta_1 SR + \beta_2 PD + \beta_3 Nfix + \beta_4 BiomassCV + \beta_5 Age + \beta_6 Eco + \beta_7 PT + \pi_{study} + \pi_{obsID} + \varepsilon \quad (8)$$

where SR is species richness; PD is phylogenetic diversity; Nfix is mixing with N-fixing species; BiomassCV is the coefficient of variation of monoculture biomass of different species; Age is the stand age of the biomass measurement; Eco is the ecosystem type; and PT is the plant type. The tests of individual coefficients and CIs are based on a t -distribution by specifying test = “t”. To overcome the issue of non-independence among the weights in the same study, we implemented the RVE algorithms for all meta-regression models⁷⁰. Bivariate relationships among these factors were also examined (Extended Data Fig. 10).

When we analysed the influence of the community functional properties, we used sub-datasets that contained the functional diversity and CWM based on leaf N or SLA; that is, the observations with leaf N or SLA data available of all species in mixtures (Extended Data Fig. 1a). When we analysed the influence of climatic factors, including MAT and aridity index, we used a sub-dataset that only included the observations from the field experiments (Extended Data Fig. 1a). The average NE, CE and SE were similar between different datasets (Supplementary Table 10).

Our results showed inequality as the primary factor for SE. However, the SE, calculated as the covariance between changes in the relative yields in mixture and monoculture biomass, shared a mathematically inherent relationship with the biomass difference in monocultures. When the SEs are generally positive across all observations, there is an inherent positive relationship between the SE and inequality (Extended Data Fig. 3a,b). To investigate our ecological hypothesis that higher inequality promotes positive SEs, irrespective of the mathematical

relationship, we created a modified selection effect (SE_{modified}) that excludes the effect of the absolute values of the difference in species biomass:

$$SE_{\text{modified}} = \sum_i \left((\Delta RY_i - \overline{\Delta RY}) \times \frac{M_i - \overline{M}}{|M_i - \overline{M}|} \right) \quad (9)$$

which no longer shared an inherent mathematical relationship with inequality (Extended Data Fig. 3c). Then we examined the relationship between SE_{modified} and inequality across our dataset (Extended Data Fig. 4).

Publication bias may be potentially introduced into the meta-analyses of BEF as a result of several reasons including: (1) BEF studies usually indicate positive BEF and those reporting positive BEF may be more easily published and retain higher visibility; and (2) some studies may selectively report the results of the mixtures with stronger mixture or diversity effects. To lower the publication bias, we (1) included plant mixture studies with different targets, not only the studies focusing on BEF, but also those focusing on interspecific versus intraspecific competition; (2) included data from theses and non-English sources, which may report a higher proportion of non-significant or contradictory results; (3) examined the raw data of the literature and used the complete data of different plant mixtures when available. Additionally, we examined the publication bias for the plant mixture effect using a modification of Egger's regression test⁷⁶: we fitted a mixed-effect model to the plant mixture effect with the substituted sampling variance in this study, corrected $1/W_r$, as a moderator. The result showed a non-significant variation of plant mixture effects with corrected $1/W_r$ ($P > 0.05$), indicating limited publication bias. We also analysed the fail-safe number (Rosenberg's N) for potential publication bias to influence our results⁷⁷. The fail-safe number for the NE is 908,131, which is far above the threshold of 23,000 ($5 \times n + 10$); that is, the threshold for robust significant meta-analytic result⁷⁷. R packages including metafor⁶⁹, taxize⁵⁶, VPhyloMaker⁵⁷, FD⁶⁴, lme4⁷⁸, lmerTest⁷⁹, multcomp⁸⁰, ggplot2⁸¹ and cowplot⁸² were used to assist with graphing and statistical analyses, which were conducted in R v.4.3.2 (ref. 83).

Reporting summary

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

Data availability

The source data underlying Figs. 2–5, Extended Data Figs. 1–10 and Supplementary Tables 1–4 and 8–11 are available via Figshare at <https://doi.org/10.6084/m9.figshare.27316062> (ref. 53). The plant trait data are available from the TRY database (www.try-db.org/).

Code availability

The R scripts needed to reproduce the results are available via the Figshare repository at <https://doi.org/10.6084/m9.figshare.27316062> (ref. 53).

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Author contributions C.C. and H.Y.H.C. designed the research. C.C. and W.X. collected the data. C.C. and W.X. performed the analysis and wrote the first draft of the manuscript. C.C., W.X. and H.Y.H.C. wrote interactively through several rounds of revisions.

Competing interests The authors declare no competing interests.

Additional information

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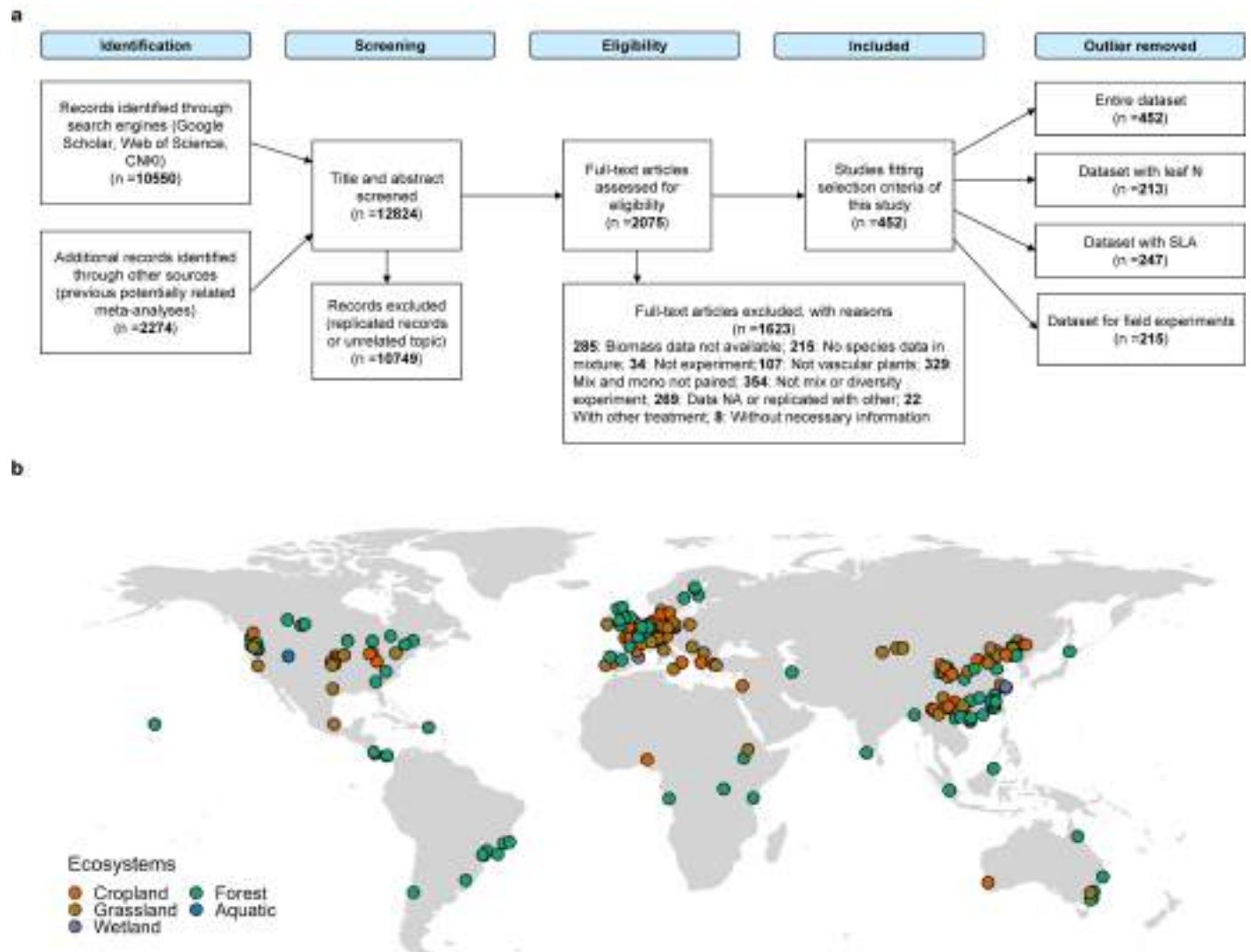
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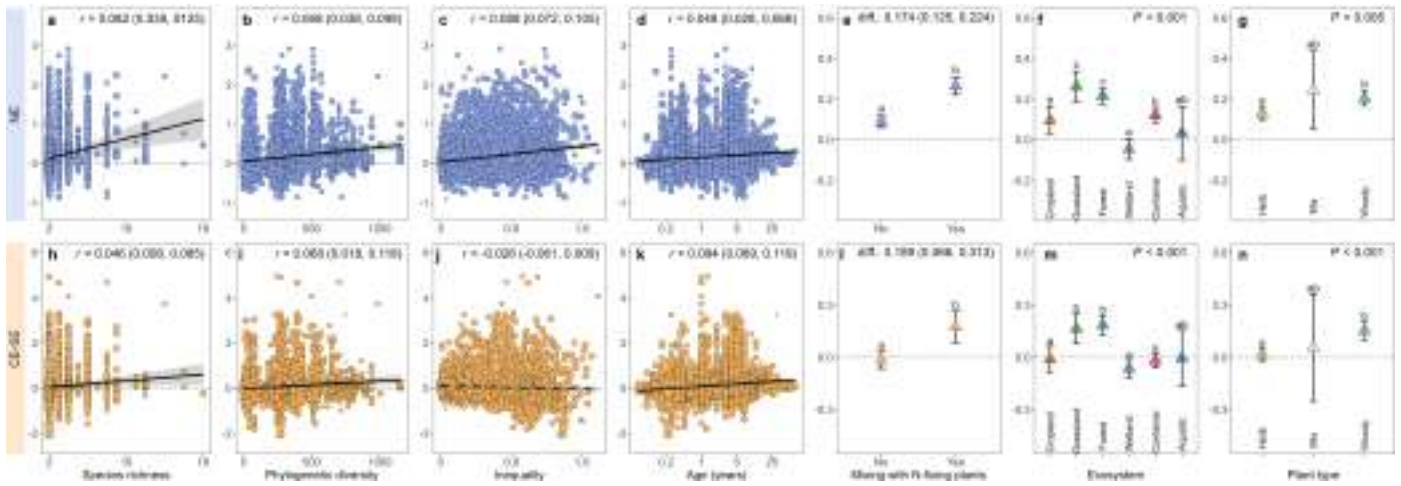
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Extended Data Fig. 1 | Data collection for this meta-analysis. a, PRISMA diagram showing the process of locating studies included in the dataset of this study; **b**, Global distribution of field experiments included in this

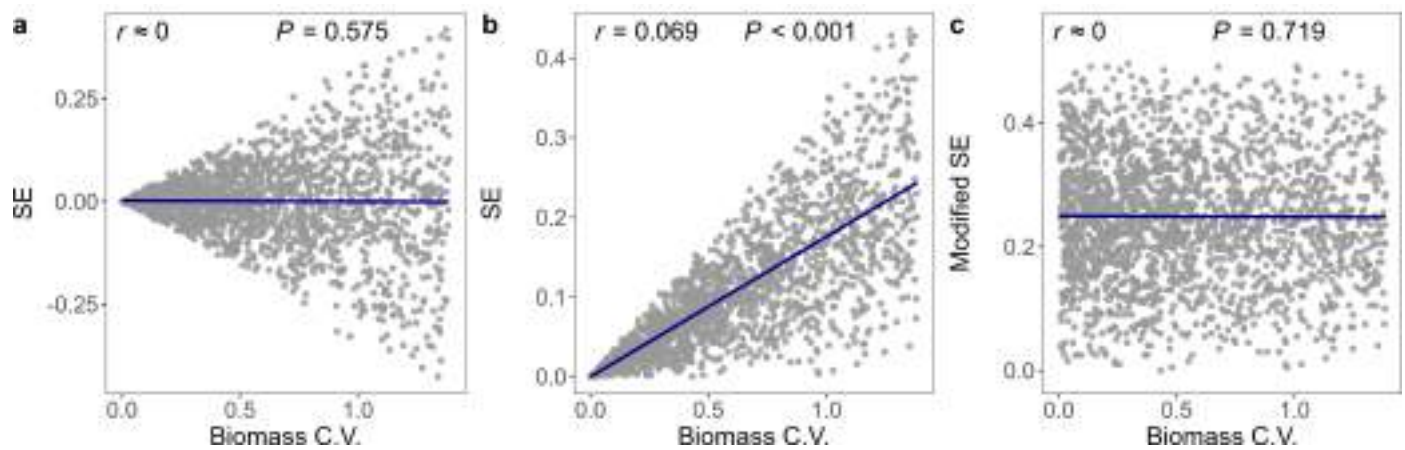
meta-analysis. Credits: schematic in **a** adapted with permission from ref. 50, Cambridge Philosophical Society; map in **b** adapted from Natural Earth project (naturalearthdata.com) under a Creative Commons licence CC0 1.0.



Extended Data Fig. 2 | Potential predictors explaining NE and CE - SE.

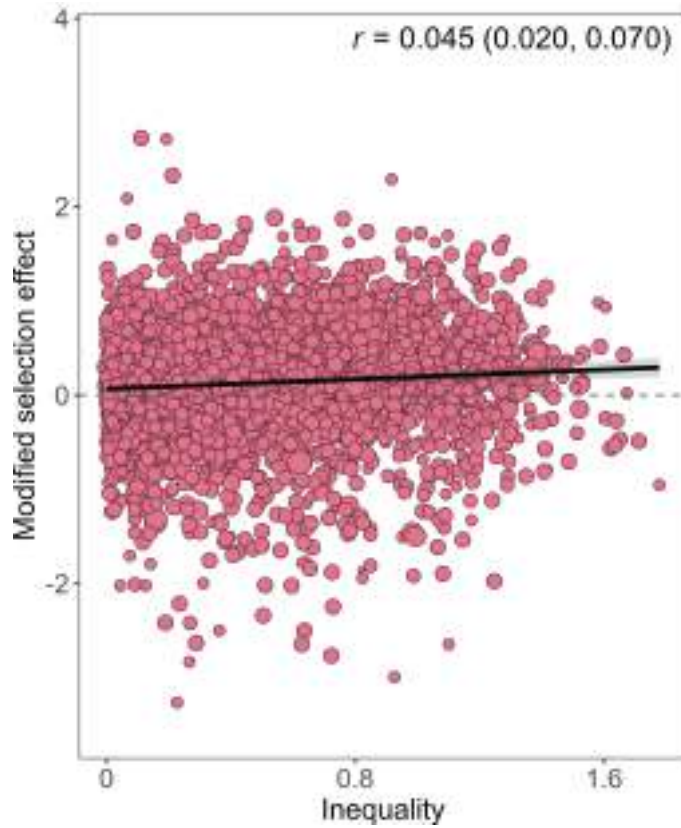
The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models followed by robust variance estimation (RVE), based on the entire dataset of plant mixture observations ($n = 4598$). In **a-d** and **h-k**, the regression line represents the response to a predictor with the 95% confidence interval (CI) shaded, and the values of the estimated coefficient and 95% CI are shown in each subplot; circle sizes are proportional to the relative weights of the observations. In **e-g** and **i-n**, the mean NE or CE - SE and 95% CIs are shown for mixing and not mixing with N-fixing plants (1934 and 2664 observations, respectively), among ecosystems of cropland, grassland, forest,

wetland, container and aquatic systems (865, 1286, 902, 18, 1387, 140 observations, respectively), among plant types of herbs, mixtures of herbs and woody plants and woody plants (3522, 58, 1018 observations, respectively); the P values of the multiple comparison are adjusted with Benjamini-Hochberg procedure, with significant difference ($P < 0.05$) marked as different letters; exact P values for **f** and **m-n** are 8.4×10^{-15} , 6.6×10^{-11} and 9.9×10^{-5} , respectively. NE: relative net biodiversity effect; CE - SE: difference between relative complementarity effect and relative selection effect. In **g-h**, the plant mixtures are classified into herbaceous plants, woody plants, and mixtures of both herbaceous and woody plants.

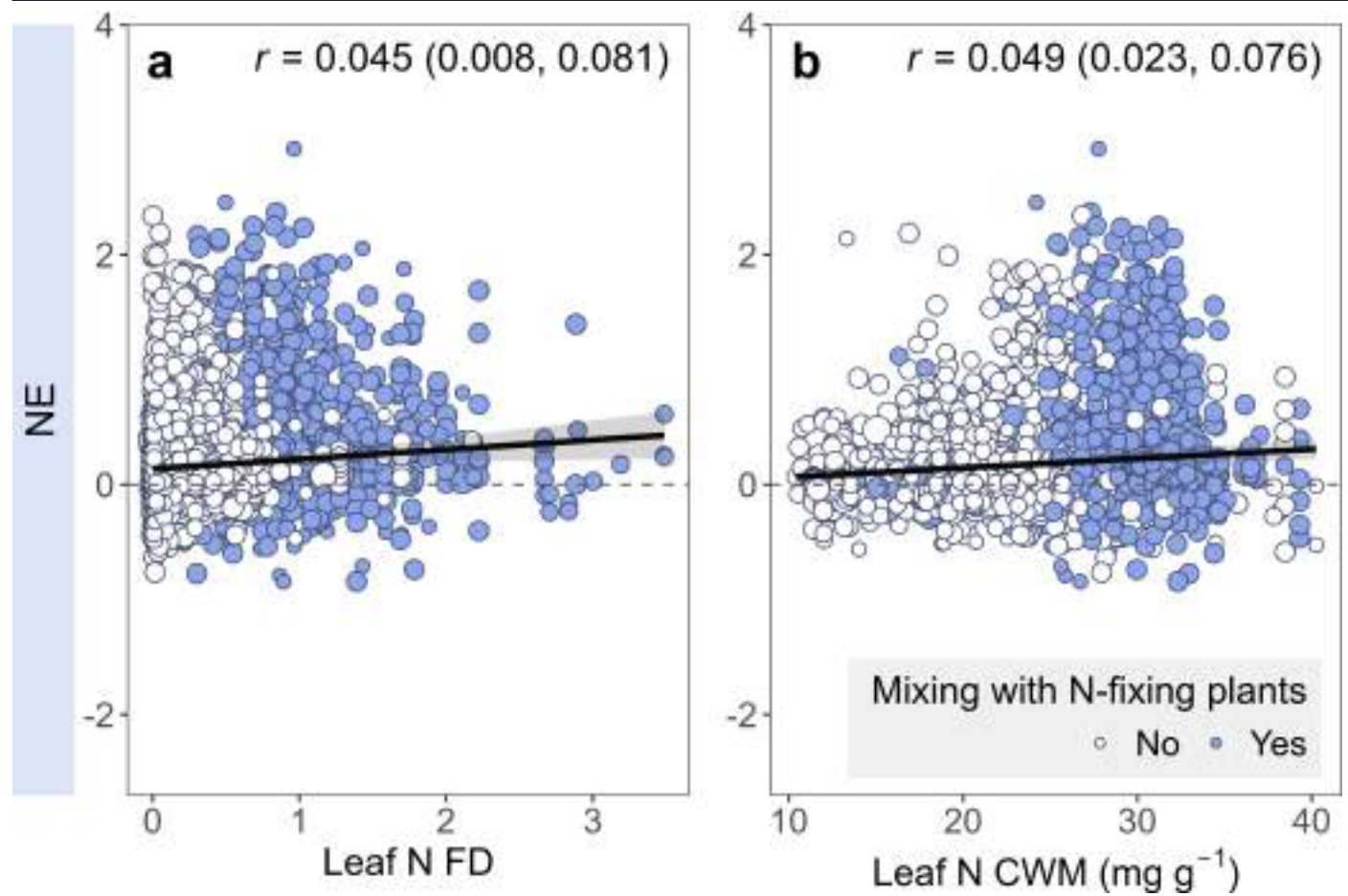


Extended Data Fig. 3 | Simulated data showing the relationships between selection effects and the coefficient of variation (C.V.) of monoculture biomass. **a**, The non-significant trend between the selection effect and inequality assuming that all individuals increased randomly by 1% to 100% in the mixtures, that is, the selection effects are random around 0; **b**, The strong positive relationship between the selection effect and inequality assuming that all species of higher productivity increased randomly by 51% to 100%, and the species of lower productivity increased randomly by 1% to 50% in the mixtures, i.e., the selection effects are positive; **c**, the non-significant trend between

“modified selection effects” (see details in Data analysis) and inequality with the same assumption of positive selection effects as in **b**. The coefficient of variation (C.V.) of monoculture biomass indicates the inequality of species biomass in monocultures. The simulation was conducted with 2000 pairs of mixtures and their corresponding monocultures, with the biomass of species biomass in monocultures randomly assigned between 1 and 100. Their relationships were examined using simple linear models. The *P* value in **b** is less than 2.2×10^{-16} .

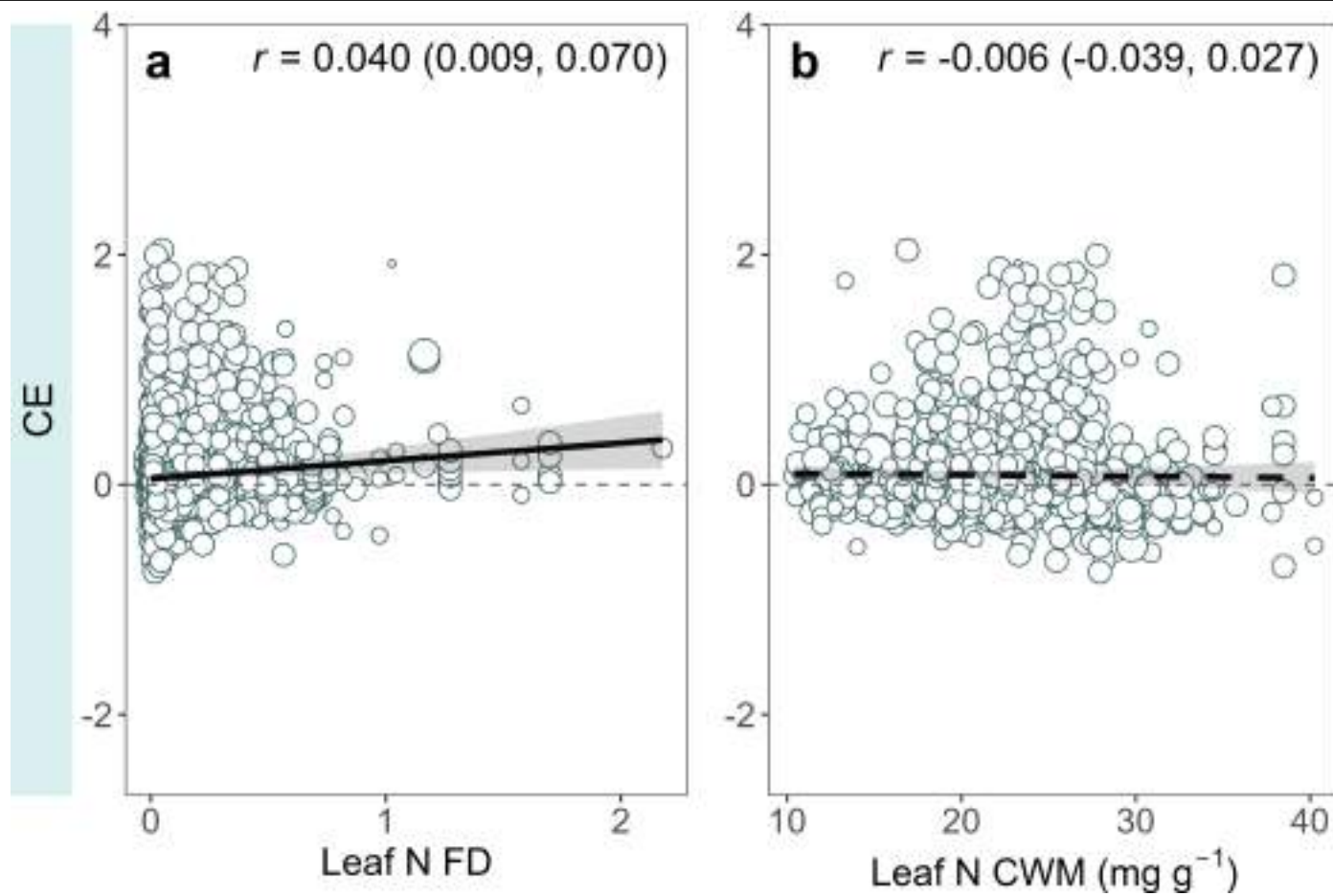


Extended Data Fig. 4 | Bivariate relationship between species biomass inequality of monocultures and the modified selection effect. Inequality was measured as the coefficient of the variation of monoculture biomass of plant species. The modified selection effect was calculated to exclude the effect of the absolute value of biomass difference (see details in Data analysis). The relationship is evaluated using a two-sided t-test in the mixed-effect meta-regression model followed by robust variance estimation (RVE), based on the entire dataset of observations of plant mixtures ($n = 4598$). The regression line represents the response to the predictor with the 95% confidence interval (CI) shaded, and the values of the estimated coefficient and 95% CI are shown; circle sizes are proportional to the relative weights of the observations. The exact P value of the relationship is 5×10^{-4} .



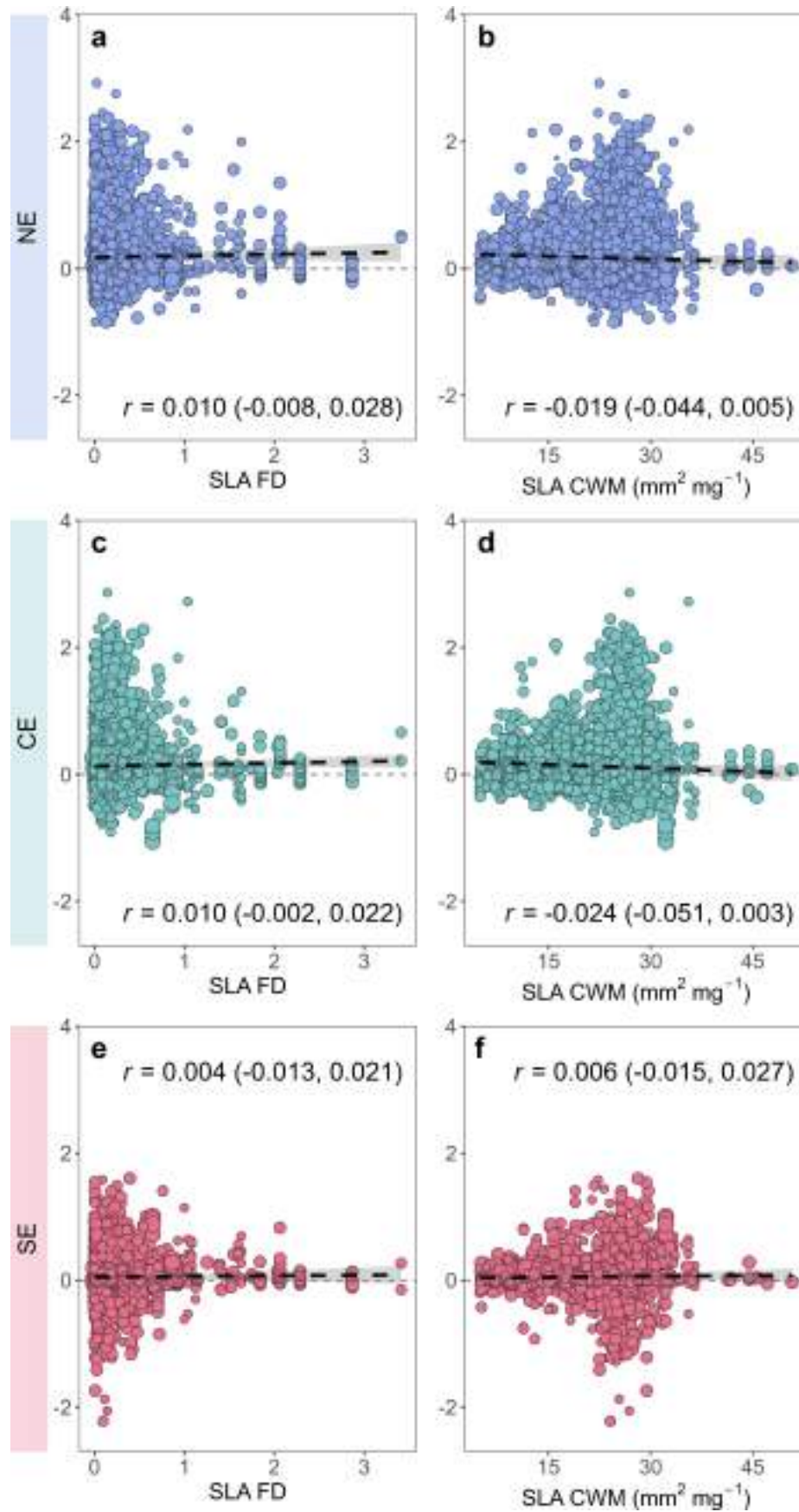
Extended Data Fig. 5 | Bivariate relationships between NE and functional characteristics based on leaf N content. The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models followed by robust variance estimation (RVE), based on the plant mixture observations with leaf N content ($n = 2273$). The regression line represents the response to a predictor with the 95% confidence interval (CI) shaded, and the values of the

estimated coefficient and 95% CI are shown in each subplot. Observations with the mixing of N-fixing and non-N-fixing species were highlighted as darker colours. The sizes of the circles are proportional to the relative weights of the observations. NE: relative net biodiversity effect; FD: functional diversity, measured as Rao's Q ; CWM: community-weighted mean.



Extended Data Fig. 6 | Bivariate relationships between CE and functional characteristics based on leaf N content for observations without the mixing of N-fixing and non-N-fixing plants. The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models followed by robust variance estimation (RVE), based on the plant mixture observations

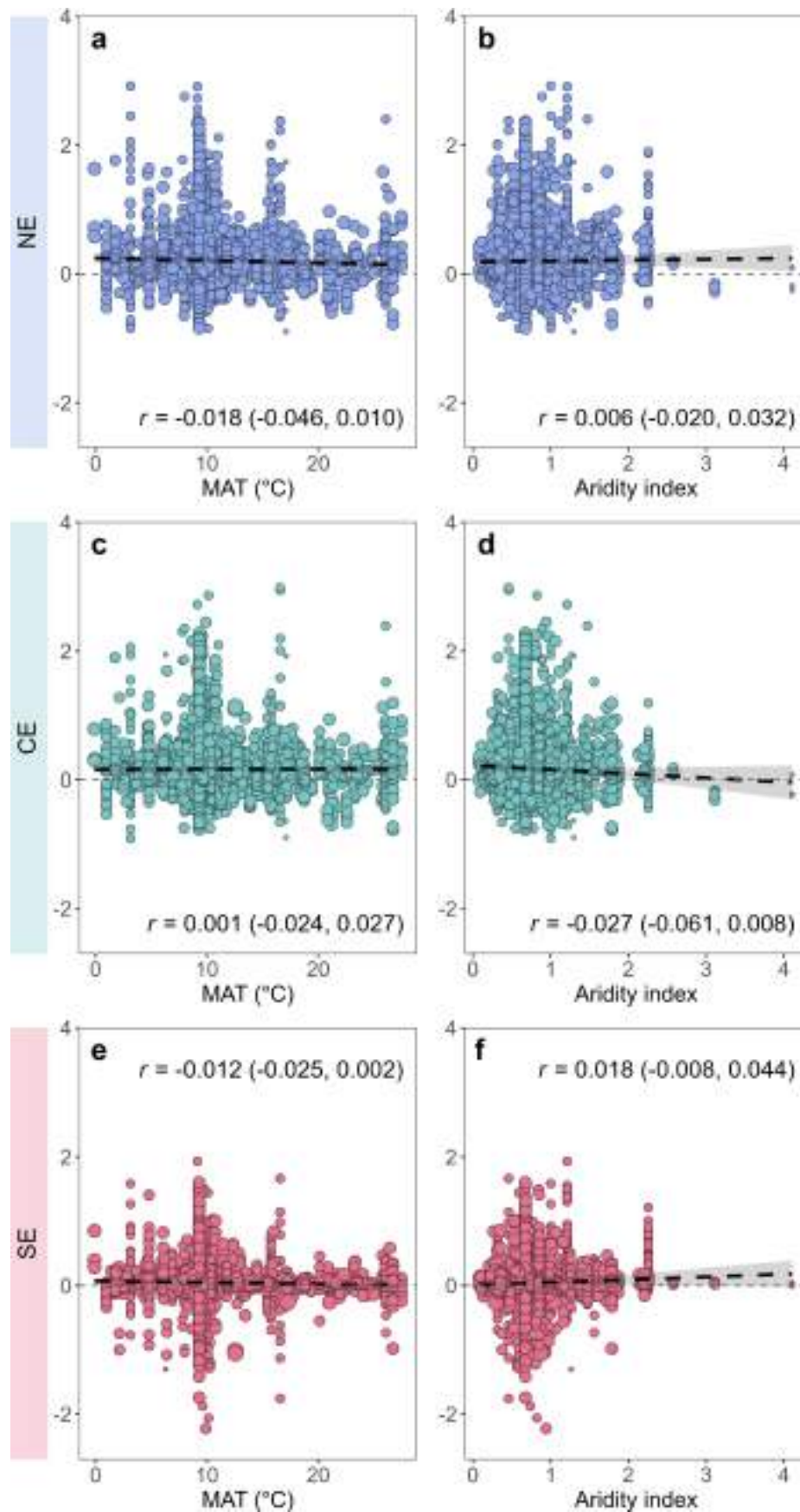
with leaf N content and without the mixing of N-fixing and non-N-fixing plants ($n = 1398$). The regression line represents the response to a predictor with the 95% confidence interval (CI) shaded, and the values of the estimated coefficient and 95% CI are shown in each subplot. The sizes of the circles are proportional to the relative weights of the observations. CE: relative complementarity effects.



Extended Data Fig. 7 | See next page for caption.

Extended Data Fig. 7 | Bivariate relationships between diversity effects and functional characteristics based on specific leaf area (SLA). The relationships are evaluated using two-sided t-tests in mixed-effect meta-regression models followed by robust variance estimation (RVE), based on observations of the plant mixtures with SLA ($n = 2784$). The regression line represents the response to a predictor with the 95% confidence interval (CI)

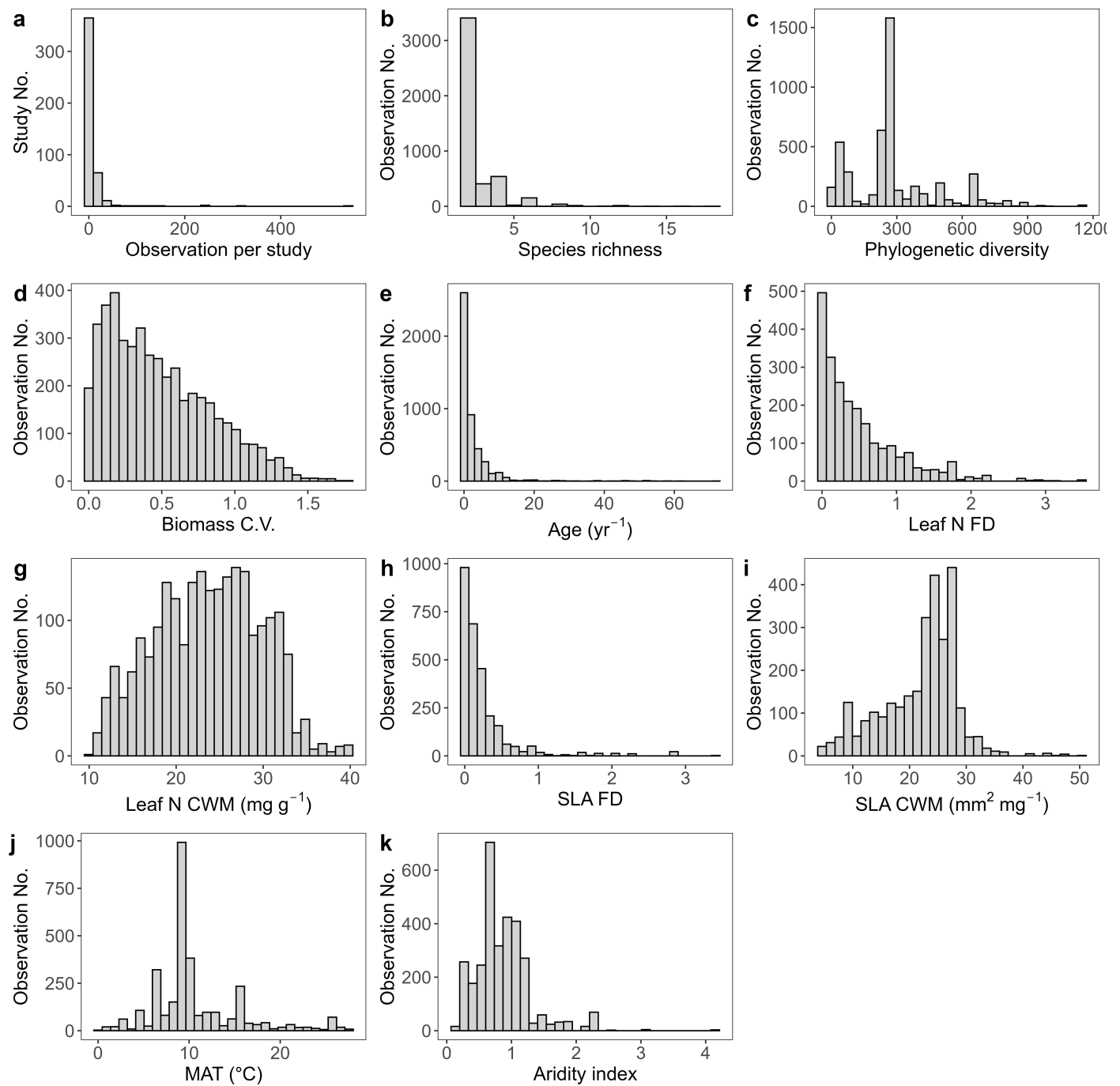
shaded, and the values of the estimated coefficient and the 95% CI are shown in each subplot. The sizes of the circles are proportional to the relative weights of the observations. NE, CE and SE: relative net biodiversity effects, complementarity effects and selection effects; FD: functional diversity measured as Rao's Q ; CWM: community-weighted mean.



Extended Data Fig. 8 | See next page for caption.

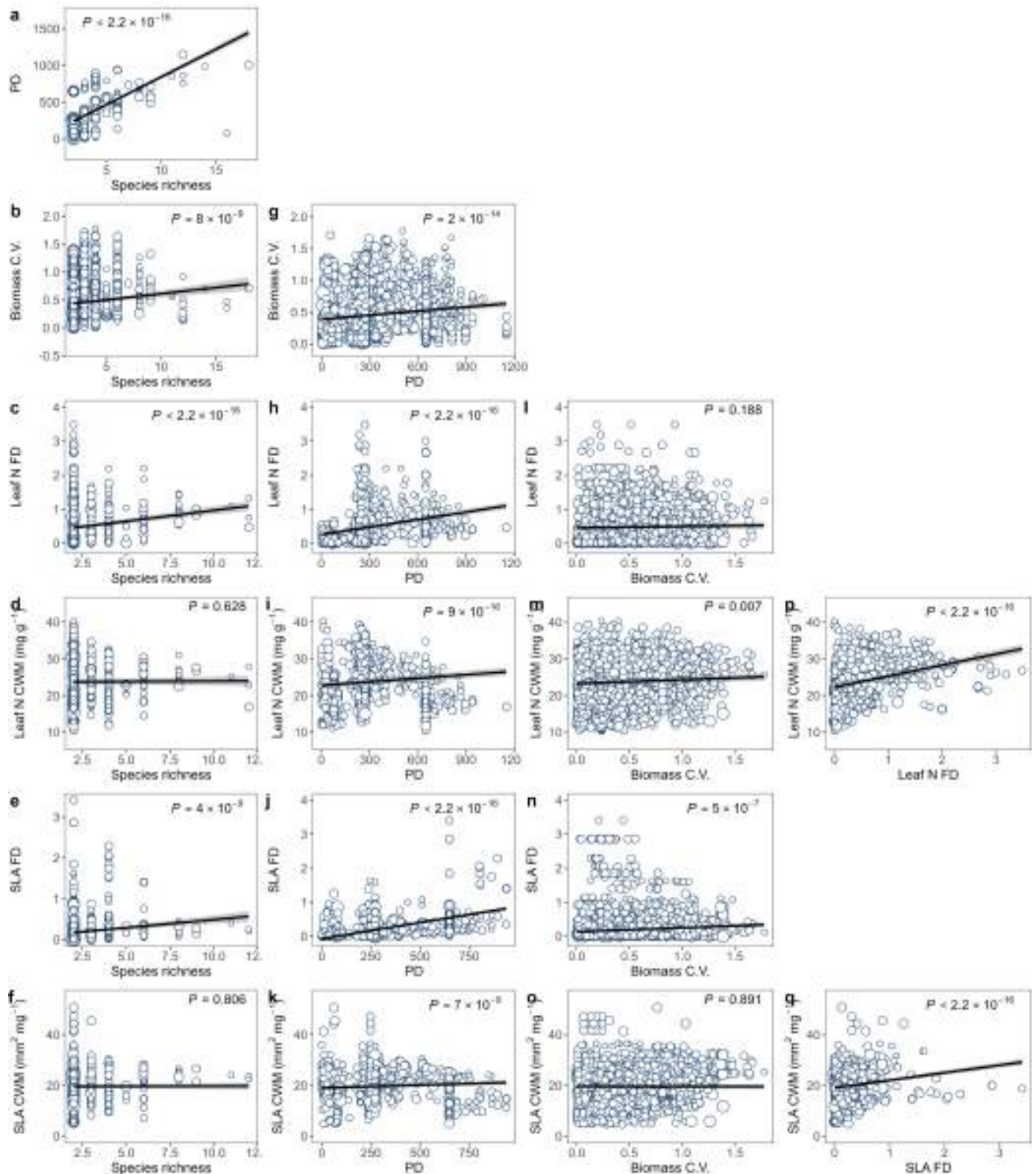
Extended Data Fig. 8 | Climate factors for NE, CE and SE. The relationships are evaluated using two-sided t-tests in mixed-effects meta-regression models followed by robust variance estimation (RVE), based on observations of the plant mixtures in the field ($n = 3091$). The regression line represents the response to a predictor with the 95% confidence interval (CI) shaded, and the

values of the estimated coefficient and the 95% CI are shown in each subplot. The sizes of the circles are proportional to the relative weights of the observations. NE, CE and SE: relative net biodiversity effects, complementarity effects and selection effects, respectively; MAT: mean annual temperature.



Extended Data Fig. 9 | Frequency distributions of observation number per study and continuous variables. **a**, Number of observations per study; **b-e**, Species richness, phylogenetic diversity, inequality of monoculture biomass and age in the entire dataset ($n = 4598$); **f-g**, Functional diversity (FD, measured

as Rao's Q) and community-weighted mean (CWM) of leaf N content in the dataset with leaf N content ($n = 2273$); **h-i**, FD and CWM of specific leaf area (SLA) in the dataset with SLA ($n = 2784$); **j-k**, MAT and aridity index in the field dataset ($n = 3091$).



Extended Data Fig. 10 | Bivariate relationships between plant mixture characteristics. The regression line is shown for the relationship of each pair of variables with the corresponding 95% confidence interval (CI) shaded. The relationships were examined using linear mixed-effects models with the random factor of 'study'. The relationships between phylogenetic diversity (PD), species richness and the inequality of monoculture biomass (measured as

coefficient of variation, C.V.) are based on the entire dataset ($n = 4598$). The relationships with FD (functional diversity, measured as Rao's Q) and CWM (community-weighted mean) of leaf and SLA are based on the dataset with leaf N ($n = 2273$) and SLA ($n = 2784$), respectively. The sizes of the circles are proportional to the relative weights of the observations.

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Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

- | | |
|-------------------------------------|--|
| n/a | Confirmed |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The exact sample size (<i>n</i>) for each experimental group/condition, given as a discrete number and unit of measurement |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> The statistical test(s) used AND whether they are one- or two-sided
<i>Only common tests should be described solely by name; describe more complex techniques in the Methods section.</i> |
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| <input type="checkbox"/> | <input checked="" type="checkbox"/> For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted
<i>Give P values as exact values whenever suitable.</i> |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

- | | |
|-----------------|--|
| Data collection | Plot Digitizer version 2.0 (Department of Physics at the University of South Alabama, Mobile, AL, USA) |
| Data analysis | The data analysis was conducted in R (v. 4.3.2), using packages including 'taxize', 'V.PhyloMaker', 'FD', 'metafor', 'lme4', 'lmerTest', 'multcomp', 'ggplot2' and 'cowplot'. The R scripts needed to reproduce the results are archived in Figshare (10.6084/m9.figshare.27316062). |

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

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The source data underlying Figs. 2–5, Extended Data Figures and Supplementary Tables are archived in Figshare (10.6084/m9.figshare.27316062). The plant trait data are available from the TRY Plant Trait Database ([www.try-db.org/](#)).

Research involving human participants, their data, or biological material

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Reporting on sex and gender N/A

Reporting on race, ethnicity, or other socially relevant groupings N/A

Population characteristics N/A

Recruitment N/A

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Study description

We conducted a global meta-analysis based on observations from 452 studies with paired observations of plant mixtures and corresponding monocultures, to evaluate net biodiversity effects and the components, i.e., complementarity effects and selection effects across global biodiversity experiments. We used mixed-effect meta-regression models to investigate the important drivers for the complementarity effects and selection effects among potential factors, including species richness, phylogenetic diversity, functional diversity, presence of contrasting N-fixing plants, species biomass inequality, community-weighted-mean of functional traits, stand age, ecosystem types, and climatic factors.

Research sample

In total, we obtained 4680 paired observations of biomass of all species in plant mixtures and corresponding monocultures from 452 studies across different ecosystem types, including grasslands (60 studies), forests (112 studies), wetlands (3 studies), croplands (42 studies), containers (213 studies), and aquatic systems (25 studies) (Extended Data Fig. 1; Supplementary Table 8); and plant types, including woody plants, herbaceous plants, and mixtures with both woody and herbaceous plants. We obtained plant biomass, species identity, species richness, species proportion, stand age, geographical location (latitude and longitude), ecosystem type, plant type and climates for each observation (Extended Data Fig. 9; Supplementary Table 9). The biomass of each species in mixtures and monocultures was recorded or calculated as the mean value across replicates. We included several studies that reported annual biomass productivity (or growth rate) of trees, which is strongly and positively related to their biomass at a young age. The biomass was estimated as the total or aboveground biomass or productivity, the carbon stock of the trees, the volume of wood or the basal area in the original studies. The biomass measured for individuals was converted to area-based with the density of the species in individual plots. The designed proportions of species in the plant mixtures were recorded as the proportions of seedlings or seeds. The plant mixtures with both non-N-fixing plants and N-fixing plants, including Fabaceae species and N-fixing actinorhizal plants, were marked as the mixing of N-fixing and non-N-fixing species. Inequality was indicated as the coefficient of variation (CV) of species biomass of their corresponding monocultures. Stand age referred to the years between the establishment of the stand or the beginning of the experiment and the measurement of biomass. For field experiments, the mean annual temperature (MAT) was recorded from the literature if available; otherwise, it was derived from the WorldClim version 2.1 dataset. To indicate the climatic water condition of each experimental location, we derived the aridity index, i.e., the ratio of the mean annual precipitation to mean annual potential evapotranspiration, from the WorldClim dataset.

Sampling strategy

To ensure the quality of the dataset, we established several criteria to determine whether each study can be included in our dataset: (a) The effects of plant diversity or mixture are isolated from other factors or treatments. (b) The planting densities of plant mixture and monoculture were constant following the substitutive design. For example, if a species was planted as 120 ind m⁻² in its monoculture, it should be planted as 40 ind m⁻² in a 1:1:1 three-species mixture. (c) No barrier between plant individuals was set up in plant mixtures or monocultures. (d) Biomass of each species in mixtures and corresponding monocultures are available in text, tables or figures. (e) The data were recorded only once if they were repeatedly reported in multiple papers. To investigate as various species combinations as possible, we included not only studies focusing on BEFs but also studies examining interspecific competition or interactions, even between species of the same genus, as long as their experimental designs fell in our data selection criteria as above.

Data collection

We followed the guidelines of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) to build up the dataset for net biodiversity effect, complementarity effect, and selection effect in manipulated plant mixture or diversity experiments (Extended Data Fig. 1a; Supplementary Table 5). Specifically, we first searched for all peer-reviewed journal articles and theses for

related studies using the Web of Science (Core Collection; <http://www.webofknowledge.com>), Google Scholar (<http://scholar.google.com>), and the China National Knowledge Infrastructure (CNKI; <https://www.cnki.net>) until December 1, 2023. We employed different combinations of keywords, including (species diversity OR species richness OR plant mixture OR plant diversity OR tree mixture OR mixed plantation OR pure and mixed) AND (biomass OR growth OR productivity OR basal area OR overyielding OR complementarity effect OR selection effect OR sampling effect OR competition). Additionally, we investigated all studies citing de Wit (1960), whose replacement series design is widely used in plant mixture or diversity manipulation experiments. We also examined the datasets of previous syntheses and meta-analyses with related topics as supplementary data sources (Supplementary Table 6). Two of the three authors independently followed the guidelines of PRISMA, searched the different combinations of keywords, and examined each related literature against the data selection criteria. 37 studies that were only selected by one of the authors were more carefully and interactively examined by the two authors to determine their inclusion following data selection criteria. All the unselected literature was listed with the reasons for exclusion (Extended Data Table 7).

Timing and spatial scale	The publications included in the dataset ranged from 1962 to 2023. The observations were distributed across the globe.
Data exclusions	Observations were excluded if not following our established criteria: (a) The effects of plant diversity or mixture are isolated from other factors or treatments. (b) The planting densities of plant mixture and monoculture were constant following the substitutive design. For example, if a species was planted as 120 ind m ⁻² in its monoculture, it should be planted as 40 ind m ⁻² in a 1:1:1 three-species mixture. (c) No barrier was established between plant individuals in mixtures or monocultures. (d) Biomass of each species in mixtures and corresponding monocultures are available in text, tables or figures. (e) The data were recorded only once if they were repeatedly reported in multiple papers. As outliers are present in diversity manipulation experiments and affect the validity of the conclusions from a meta-analysis, any ΔY , CE and SE with a standardized residual value exceeding the absolute value of three were removed as outliers.
Reproducibility	All attempts to repeat the analysis and results were successful.
Randomization	N/A
Blinding	Blinding was not possible in the data analysis.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

Methods

- n/a Involved in the study
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 - ☒ ☐ Eukaryotic cell lines
 - ☒ ☐ Palaeontology and archaeology
 - ☒ ☐ Animals and other organisms
 - ☒ ☐ Clinical data
 - ☒ ☐ Dual use research of concern
 - ☒ ☐ Plants

- n/a Involved in the study
- ☒ ☐ ChIP-seq
 - ☒ ☐ Flow cytometry
 - ☒ ☐ MRI-based neuroimaging

Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A