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Reconciling biodiversity–ecosystem functioning relationships across systems

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Reconciling biodiversity–ecosystem functioning relationships across systems

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Abstract

It remains unresolved why biodiversity experiments consistently yield positive biodiversity–ecosystem functioning relationships, with species performing better, on average, in species-rich than in species-poor communities[1–5], whereas natural communities often show mixed patterns[6,7]. To address this gap, we developed a framework applicable to both systems that partitions ecosystem functioning into average and covariance effects arising from proportionate and abundance-dependent disproportionate species contributions, respectively. Across both systems, ecosystem functioning was positively related to both effects, and species diversity was positively associated with the average effect but negatively associated with the covariance effect. In natural communities, a strong covariance effect generated mixed or sometimes negative biodiversity–ecosystem functioning relationships, including under nitrogen addition[8–11], whereas in biodiversity experiments, its low relative importance, resulting from the assembly of species with controlled abundances[12–14], maintained positive relationships. This framework reveals shared underlying mechanisms and reconciles discrepant biodiversity–ecosystem functioning relationships across the two systems.

Key words: Ecosystem multi-functionality; Ecosystem stability; The Price equation; Species-area relationship; Mass-ratio hypothesis; Neutral theory

Main

Human-driven global changes[15,16] have caused rapid species losses and substantial shifts in species composition of plant communities[11,17–19], raising widespread concerns about the consequences for ecosystem functioning[20–22]. To investigate the mechanisms underlying ecosystem functioning, manipulative biodiversity experiments assemble mixture communities with varying numbers of species randomly drawn from a common species pool that also includes monocultures[12,14]. These experiments have consistently shown that, on average, species perform better in species-rich than in species-poor communities, leading to positive biodiversity–ecosystem functioning relationships[1–5]. In natural ecosystems, however, the predicted positive relationship has been supported in some studies[23,24] but has been found to be weak or mixed in others[6,7]. Studies have also shown that ecosystem functioning under natural conditions is weakly affected by species removal diversity[25,26] and the removal of subordinate species[27], and can even increase despite species losses under nitrogen enrichment[8–11]. This discrepancy has led to longstanding debates about the extent to which biodiversity experiments represent real-world ecosystem dynamics[28–31], although other studies have supported their representativeness[32–34]. Reconciling these contrasting patterns requires a unified framework that is applicable across diverse contexts and can explain how increases in ecosystem functioning may be accompanied by either increases or decreases in species diversity, thereby giving rise to divergent biodiversity–ecosystem functioning relationships.

Motivated by the consistent application of community temporal stability across diverse systems[11,22,35], we developed a framework to address this gap. This framework partitions temporal deviations in ecosystem functioning (*i.e.*, anomalies) into two components: one reflecting random fluctuations among species and their average performance, as assumed by theoretical studies[21,36–38] and primarily examined in biodiversity experiments[1–5], and the other

capturing non-random fluctuations (Box 1). This partitioning framework can be interpreted analogously to the endemics–area relationship under scenarios that either disregard or account for species-specific spatial distributions of individuals, and predicts high detectability of highly abundant species[39]. Consider an intact habitat of size a and a subset area of size a'. When individuals of different species are spatially randomly distributed, or are equally treated as in the neutral model[40], all species retain the same proportion of individuals (*i.e.*, a'/a) within the subset area[39]. Under this scenario, only the average effect (term) arises, because no species is preferentially concentrated within (or excluded from) the subset area, and consequently, the covariance effect (term) between the proportions of species occurring within the subset area and their abundances is zero[39] (Box 1–Figure 1). In contrast, non-random or species-specific spatial distributions yield a non-zero covariance effect (term), capturing abundance-dependent compositional changes[39] (Box 1–Figure 1). A positive average effect increases species abundances and their detectability, and thereby species diversity, without altering abundance evenness. A positive covariance effect, however, emerges when species composition shifts toward increasing dominance of already abundant species and further rarity of subordinate species. This shift increases total abundance and species-abundance unevenness, while reducing the detectability of subordinate species, ultimately leading to lower species diversity. Conversely, a negative covariance effect arises when subordinate species increase and dominant species decline, reducing species-abundance unevenness, increasing the detectability of subordinate species, and ultimately increasing species diversity, despite a decline in total abundance.

In this study, we collected plant community data from 90 natural grasslands, of which 33 were from northern China and 57 from the Nutrient Network[41–43] (Supplementary Table 1–2, Supplementary Figure 1–2). We also compiled data from 20 biodiversity experiments (19 sites

from the Agrodiversity experiment[13] plus data from the Jena experiment[44]) (Supplementary Figure 2). We applied the partitioning framework to both natural and biodiversity experimental datasets to quantify the average and covariance effects, and examined whether the two effects showed consistent patterns in shaping species diversity and ecosystem functioning across the two systems. Although a long-term experiment combining biodiversity and nitrogen treatments has demonstrated concurrent declines in species diversity and ecosystem functioning[45], nitrogen addition in natural ecosystems has been shown to increase ecosystem functioning (*e.g.*, productivity) while reducing species diversity, particularly among subordinate species[8–11]. These contrasting responses suggest that the covariance effect may play an important role in mediating natural-community responses to nitrogen addition. We therefore applied the framework to compiled data from 37 grasslands with nitrogen addition (3 sites from northern China and 34 sites from the Nutrient Network[41,42]) (Supplementary Table 1–2, Supplementary Figure 1–2). In addition, we investigated whether species with different abundances contributed equally to the average and covariance effects, and whether the assembly of species with controlled abundances in biodiversity experiments[12–14], in contrast to the assembly processes operating in natural communities (Box 1, Supplementary Figure 3–5), underlies differences in the relative importance of the two effects in driving ecosystem functioning.

Average and covariance effects

We analyzed the average and covariance effects in affecting community structural features, including species richness and species-abundance unevenness (estimated using the Gini index), both defined as the deviation of each observed community from the reference community that explicitly represents the average across all observations (Box 1–Figure 1). To account for the tendency of communities with higher species richness to exhibit larger absolute changes

(Extended Data Figure 1a–d and 2a–b), we analyzed residual changes in species richness. Across both natural and biodiversity experimental communities, residual changes in species richness were positively associated with the average effect (Figure 1a–d, Extended Data Figure 3a–b) but negatively associated with the covariance effect (Figure 1e–h, Extended Data Figure 3c–d). Additionally, residual changes in species richness were negatively related to changes in species-abundance unevenness (Extended Data Figure 1e–h and 2c–d), which was positively associated with the covariance effect (Extended Data Figure 1i–l and 2e–f).

Using linear and subsequent residual regressions to analyze the average and covariance effects in driving ecosystem functioning (plant coverage for Nutrient-Network grasslands and productivity for others; see Methods), we found that both effects positively affected ecosystem functioning across natural and biodiversity experimental systems (Figure 2a–h and Extended Data Figure 4a–d). We then assessed their contributions to the variance in ecosystem functioning by comparing the explanatory power (*i.e.*, R^2) of the average effect from linear regressions with the partial explanatory power (*i.e.*, partial R^2) of the covariance effect derived from residual regressions (*i.e.*, its explanatory power scaled by the unexplained variance from the initial linear regression; see Methods). In natural communities, the covariance effect contributed comparably to the average effect (Figure 2i–j, Supplementary Figure 6–9), whereas in biodiversity experiments, its contribution was lower than that of the average effect (Figure 2k–l, Extended Data Figure 4e–f).

Covariance effect and nitrogen addition

We applied the partitioning framework to grassland nitrogen addition experiments (see Box 1 for detail). In the grasslands of northern China, nitrogen addition increased productivity (Figure 3a) but reduced species richness (Extended Data Figure 5a, Figure 3b). In Nutrient-

Network grasslands, nitrogen addition had neutral effects on plant community coverage (Figure 3c) while similarly increasing productivity (Extended Data Figure 6) and reducing species richness (Extended Data Figure 5b, Figure 3d). Across both datasets, nitrogen addition had neutral (Figure 3e) or negative (Figure 3g) effects on the average effect, while consistently increasing the covariance effect (Figure 3f and 3h), and both effects positively impacted ecosystem functioning (Extended Data Figure 7). Furthermore, residual changes in species richness were positively associated with the average effect (Figure 3i and 3k), but negatively associated with the covariance effect (Figure 3j and 3l). Residual changes in species richness were also negatively related to changes in species-abundance unevenness (Extended Data Figure 5c–d), which in turn was positively related to the covariance effect (Extended Data Figure 5e–f).

Abundance structure and covariance

Unlike the average effect, which was relatively strongly driven by subordinate species (comparing R_m^2 in Figure 4a and 4c with partial R_m^2 in Figure 4e and 4g), the covariance effect was unequally contributed by different species (Box 1) and was strongly driven by dominant species (comparing R_m^2 in Figure 4b and 4d to partial R_m^2 in Figure 4f and 4h). Consequently, the covariance effect was more vulnerable than the average effect to changes in species contributions arising from decreasing species-abundance unevenness (Box 1, Figure 4i–l). Accordingly, the (partial) explanatory power of the covariance effect was positively related to species-abundance unevenness (Box 1) in biodiversity experimental communities (Extended Data Figure 8c–d, Extended Data Figure 9), but showed no significant relationship in natural communities, likely because of the narrower range of unevenness (Extended Data Figure 8a–b). Furthermore, in the Agrobiodiversity experiments[13], reversing species-abundance ranks led to a reversal in the sign of

the estimated covariance effect (Box 1, Extended Data Figure 10), providing additional evidence for the sensitivity of the covariance effect to changes in species-abundance distributions.

Discussion

Our study developed a novel framework, applicable across diverse contexts, to investigate why the positive biodiversity–ecosystem functioning relationships predicted by biodiversity experiments[1–5] often diverge in natural communities[6–8,10,11]. This framework partitions temporal deviations in ecosystem functioning into two components representing random, proportionate (the average effect) and non-random, disproportionate (the covariance effect) contributions among species. We found that both effects positively influenced ecosystem functioning, but had contrasting effects on species diversity. When increases in ecosystem functioning are driven by the average effect, species diversity tends to increase, resulting in positive biodiversity–ecosystem functioning relationships. In contrast, when increases are driven by the covariance effect, species composition shifts toward greater abundance unevenness, leading to reduced species diversity. The covariance effect therefore provides a mechanistic basis for negative biodiversity–ecosystem functioning relationships and helps to explain why these relationships often diverge in natural communities[6–8,10,11]. Moreover, the predicted patterns of the two effects in shaping ecosystem functioning and species diversity were consistently observed across diverse contexts, including both natural and biodiversity experimental systems. This consistency suggests that biodiversity experiments capture key processes operating in natural communities, thereby helping to reconcile longstanding debates over their ability to represent real-world ecosystem dynamics[28–34].

In natural plant communities, we found that the covariance effect contributed to ecosystem functioning at a level comparable to the average effect, in contrast to biodiversity

experiments where the average effect typically acts as the dominant driver. Although further work is needed to validate the generality of a strong covariance effect across a wider range of natural communities, we speculate that this pattern is widespread. In natural communities, species often respond disproportionately to anthropogenic global changes, including eutrophication[9,10], grazing[8], climatic warming and changes in precipitation amount and variability[17,18]. Such disproportionate responses indicate that species performances are clustered rather than randomly distributed[39] under particular environmental conditions, leading to shifts in species composition and the emergence of the covariance effect. As a result, the covariance effect is likely to play a key role in mediating ecosystem functioning in natural communities under ongoing anthropogenic global changes.

Following this line of reasoning, we applied the partitioning framework to nitrogen addition experiments in natural grasslands and found that nitrogen addition had neutral or positive effects on ecosystem functioning (*e.g.*, productivity or coverage) while reducing species richness. These patterns were consistent with findings from previous nitrogen addition experiments[8–11]. However, the resulting neutral or negative relationships between species diversity and ecosystem functioning across treatments contrasted with the generally positive relationships reported in biodiversity experiments[1–5]. Our partitioning framework suggests that this discrepancy arises because increases in ecosystem functioning under nitrogen addition are primarily driven by the covariance effect. The concurrent increases in species-abundance unevenness and declines in species richness are also consistent with previous findings showing that nitrogen addition promotes the growth of dominant species while suppressing subordinate species, ultimately leading to species loss[8–11]. Together, these findings suggest that our partitioning framework provides mechanistic insights into how anthropogenic nitrogen

eutrophication shapes community species diversity and composition, and ultimately influences ecosystem functioning.

Our study indicates that the positive versus often mixed biodiversity–ecosystem functioning relationships observed in biodiversity experiments and natural communities do not arise from fundamentally different underlying mechanisms[28,30], but instead from differences in the relative importance of the average and covariance effects in driving ecosystem functioning. We demonstrated that the covariance effect was unevenly contributed by species and highly sensitive to abundance-associated changes in species contributions. Importantly, this pattern does not simply imply that a high relative importance of the covariance effect is necessarily associated with highly uneven species abundances. Rather, it suggests that a strong covariance effect emerges when species with above-average performance attain higher-than-average abundances (Box 1). This is likely the case in, at least, mature natural communities, where species better adapted to local environmental conditions achieve both superior performance and dominant abundance positions[29,46,47], thereby contributing to the often mixed biodiversity–ecosystem functioning relationships[6,7]. By contrast, biodiversity experiments typically assemble mixture communities with controlled species abundances[12–14], rather than reflecting the inherently uneven abundances arising from unequal species performance. This design likely reduces the contribution of species exhibiting both superior performance and high abundance under natural conditions to the covariance effect, resulting in ecosystem functioning being predominantly driven by the average effect and consequently generating positive biodiversity–ecosystem functioning relationships[1–5].

Methods

Global natural grassland dataset

The current study used two natural grassland plant community datasets (productivity and coverage) to investigate the roles of the average and covariance effects in driving ecosystem functioning. The first dataset comprised plant productivity data from northern China grasslands, primarily derived from a 17-year regional survey conducted across 30 sites in the Inner Mongolian temperate grasslands. Most sites (23 sites) were established in 2007, with the remaining 7 sites added in subsequent years (Supplementary Table 1, Supplementary Figure 1). Plant community surveys were conducted during the peak biomass season, typically between late July and early August. During each survey, living plant material was harvested from three 1 × 1 m quadrats arranged along the diagonal of a randomly selected 10 × 10 m plot, while avoiding areas subjected to intensive anthropogenic disturbances such as grazing or mowing. Harvested plant material was sorted by species to determine community species richness, then oven-dried and weighed to obtain aboveground biomass as a proxy for annual productivity. The 30 sites were resurveyed during two periods (2012–2016 and 2020–2023) following identical protocols. To broaden spatial coverage, the dataset also included plant productivity data from ambient-treatment plots in 3 long-term nutrient addition experiments (5–8 years; see below for details), with two sites located in the northeastern and central Inner Mongolian temperate grassland, and one in the northeastern Tibetan alpine grassland (Supplementary Table 1, Supplementary Figure 1). Collectively, the northern China grassland productivity dataset included 254 site-year observations.

The second dataset comprised grassland plant coverage measurements from the Nutrient Network, a globally distributed nutrient addition experiment network that follows standardized sampling protocols[41]. This dataset included plant coverage data from 57 sites, with 55 sites

obtained from one recent publication and 2 additional sites integrated from another source[42,43]. To ensure consistency, only post-treatment observations under ambient conditions were included to represent natural or semi-natural grasslands. The 57 sites spanned five continents and encompassed a broad range of grassland types across diverse climatic zones[42,43] (Supplementary Table 2, Supplementary Figure 2). Most sites included 3 replicate quadrats per site-year (except one site with 2 quadrats) and provided 4–14 years of post-treatment observations. At each site, a permanently marked 1 × 1 m quadrat within an ambient plot was used for annual visual estimation of plant coverage for all species. Total plant coverage could exceed 100% due to multilayered canopy structures. In total, this plant coverage dataset comprised 467 site-year observations.

For these natural grassland datasets, temporal deviations (*i.e.*, anomalies) in productivity (or coverage), the associated average and covariance effects, and changes in specie richness and species-abundance unevenness (estimated using the Gini index) were quantified by comparing annual community observations (averaged across quadrats or plots) with the multi-year average within the same site (Box 1).

Grassland biodiversity experiment dataset

The current study used published plant productivity datasets from two biodiversity experiments, *i.e.*, the Agrodiversity experiment[13] and the Jena experiment[44,48]. The Agrodiversity experiment dataset included 2–4 years of observations (collected between 2003 and 2011, with 1–7 measurements per year) across 33 sites distributed in Europe (32 sites) and Canada (1 site)[13]. At each site, 4 species (2 grasses and 2 legumes) were planted in monocultures and in 11 four-species mixture communities under two seeding densities (high and low, with low defined as 60% of the high density). This design resulted in a total of 30 plots per site. For each seeding

density level, the 11 four-species mixtures included one with equal planting proportions of all 4 species and ten with varying planting proportions among the 4 species[13].

The Jena experiment (data collected between 2002 and 2010, with typically 2 measurements per year) was established based on a regional species pool of 60 native grassland species[44,48] and consisted of two components, *i.e.*, the main experiment and the dominance experiment. In the main experiment, 82 plots were established with mixture communities of 2, 4, 8, 16 and 60 species randomly selected from the full species pool. The dominance experiment focused on 9 dominant species from the pool and assembled them into mixture communities of 2, 3, 4, 6 and 9 species across 206 plots.

For both biodiversity experiments, we used only data from mixture communities (plots) with at least 3 annual observations during the peak biomass season (typically August). In the Agrodiversity experiment, this criterion resulted in the inclusion of 19 sites (416 plots in total) distributed across Europe (18 sites) and Canada (1 site) (Supplementary Figure 2), yielding 1269 plot-year observations. In the Jena experiment, 253 mixture communities (plots) from both the main and dominance experiments met this criterion, yielding 2033 plot-year observations. For these biodiversity experiments, temporal deviations (*i.e.*, anomalies) in productivity, together with the associated average and covariance effects, were estimated by comparing annual observations with the multi-year average within the same mixture community (*i.e.*, plot) (Box 1).

Grassland nitrogen addition experiment dataset

We conducted 3 nitrogen addition experiments across northern China grasslands to investigate the mechanisms underlying plant community responses (Supplementary Figure 1). These experiments were located in the northeastern (Hailaer) and central (Maodeng) regions of the Inner Mongolian temperate grasslands, and in the northeastern Tibetan alpine grassland

(Haibei). The dominant vegetation types at these sites are meadow steppe (Hailaer), typical steppe (Maodeng) and alpine meadow (Haibei), respectively. All 3 experiments were established in 2011 using a coordinated randomized block design, with each experiment containing 5–6 replicate blocks. Each block was divided into six 6 m × 6 m plots, with two plots randomly assigned to either an ambient nitrogen control or a nitrogen addition treatment (10 g N m^{-2} $year^{-1}$ as urea, hand-broadcast in May, June and July each year). From 2011 to 2018, species-specific aboveground biomass was measured as a proxy for plant productivity during the peak growing season (late July to early August). At the Haibei (2011–2014 and 2017) and Maodeng (2012–2018; samples from 2011 were lost) sites, data were collected from three blocks. At the Hailaer site, data were collected from 5 blocks during 2011–2015. Biomass was harvested within a 1 m × 1 m quadrat (0.5 m × 0.5 m quadrat at Haibei), sorted by species to determine species richness, and then oven-dried and weighed to obtain species-specific productivity. In total, this dataset included 122 plot-year observations.

To extend our investigation of nitrogen addition responses beyond China grasslands, we also included plant coverage data from a recent publication[42] based on the Nutrient Network[41]. This dataset included 7 years of grassland plant coverage observations across 34 globally distributed sites (Supplementary Figure 2). These nitrogen addition experiments followed a coordinated design, with 2–6 replicate blocks per site arranged in a randomized block layout. Each block included an ambient nitrogen control plot and a nitrogen addition plot (10 g N m^{-2} $year^{-1}$ as urea). Plant coverage for all species was visually estimated annually within a permanently marked 1 × 1 m quadrat in each plot. In total, this dataset included 1552 plot-year observations.

To apply our framework to these nitrogen addition experiments, we treated plots receiving different nitrogen treatments as spatially distributed local communities, following the conceptual

framework of multi-scale temporal stability theory[49]. Accordingly, we estimated all metrics by comparing each plot-year observation with a reference community defined as the average across all plots and years within the same site (Box 1).

Statistical analysis

Built on the concept of community temporal stability, which has been consistently applied in both natural and experimental systems[11,22,35], we developed a framework to investigate the mechanisms underlying temporal deviations (*i.e.*, anomalies) in ecosystem functioning. Accordingly, these deviations were quantified by comparing each observed community with a reference community, explicitly defined as the average across all observations, and were further partitioned into components representing random, proportionate (the average effect) and non-random, disproportionate (the covariance effect) contributions among species (Box 1). Briefly, positive average effects arose from proportional increases in abundance across species and captured the associated increases in species presence probabilities and, consequently, species richness (Case 1 in Box 1–Figure 1). In contrast, positive covariance effects occurred when abundant species became increasingly dominant while subordinate species became rarer and less likely to be observed. Such compositional shifts led to more uneven species abundances and reduced species richness. When subordinate species increased and dominant species declined, a negative covariance effect arose, reducing unevenness and increasing species richness (Case 2 in Box 1–Figure 1).

We first examined the differences in species-abundance unevenness (estimated using the Gini index) between natural and biodiversity experimental communities using analysis of variance. Then, we applied the developed framework in parallel to both systems to analyze the average and covariance effects in affecting species richness, as well as the role of the covariance

393 effect in shaping the species-abundance unevenness and the influence of changes in unevenness
394 on species richness. Because communities with higher species richness could exhibit larger
395 absolute changes, we used residuals from this relationship in the analyses. We also investigated
396 the average and covariance effects in driving ecosystem functioning (productivity or coverage) in
397 both natural and biodiversity experimental communities. Linear regressions were employed to
398 analyze the impact of the average effect, with explanatory power reported as the proportion of
399 variance explained (*i.e.*, R^2; R_m^2 and R_c^2 for marginal and conditional R^2, respectively). Residual
400 regressions were used to assess the partial explanatory power of the covariance effect, calculated
401 as the product of residual-regression explanatory power and the unexplained proportion of
402 variance from the initial linear regression. These analyses were conducted using linear mixed-
403 effects models, with site (or mixture-community plot in biodiversity experiments) included as a
404 random factor to account variation in both intercepts and slopes. Linear and subsequent residual
405 regressions were also performed separately for each natural grassland site or mixture-community
406 plot. Differences between the explanatory power of the average effect and the partial explanatory
407 power of the covariance effect were assessed using paired *t*-tests within each natural grassland
408 dataset or biodiversity experimental dataset.

409 An extended version of this framework (Box 1) was applied to nitrogen addition
410 experiments in grasslands of northern China and the Nutrient Network. The effects of nitrogen
411 addition on ecosystem functioning (productivity or coverage), residual changes in species
412 richness (see above), and the average and covariance effects were analyzed using analysis of
413 variance based on linear mixed-effects models, with site and block combined into a single
414 random factor. We also analyzed residual changes in species richness in relation to the average
415 and covariance effects, as well as the role of the covariance effect in shaping species-abundance
416 unevenness and the influence of changes in unevenness on species richness. In addition, the

417 average and covariance effects in driving ecosystem functioning were analyzed using linear
418 regressions and residual regressions, respectively (see above). These regressions were conducted
419 using linear mixed-effects models, with site and block combined into a single random factor to
420 account for their influence on both intercepts and slopes.

421 In natural communities, we assessed the differential sensitivities of the average and
422 covariance effects to species-abundance distributions by separating each effect into contributions
423 from dominant species (those with cross-year average relative species biomass or coverage > 5%)
424 and subordinate species (Box 1). Contributions from dominant species were analyzed using linear
425 regressions, with explanatory powers reported, whereas contributions from subordinate species
426 were analyzed using residual regressions, with partial explanatory powers reported. To further
427 test this sensitivity, we artificially reduced species-abundance unevenness in the reference
428 community by applying geometric transformations with exponents of 1/2, 1/4, 1/8, and 1/16,
429 while preserving the original species-abundance ranks. The similarity between recalculated
430 average and covariance effects and original average and covariance effects was quantified using
431 explanatory power (R_m^2 only) from linear regressions. These regressions were conducted using
432 linear mixed-effects models, with site included as a random factor to account for its potential
433 influence on both intercepts and slopes.

434 For both natural and biodiversity experimental communities, we examined how species-
435 abundance unevenness influenced the (partial) explanatory power of the covariance effect on
436 ecosystem functioning (Box 1) using within-site (or within-mixture-community) estimations.
437 Linear regressions were applied to natural communities, whereas linear mixed-effects models
438 were used for biodiversity experiments, with site (Agrodiversity experiment) or experiment type
439 (main and dominance experiments in the Jena biodiversity experiment) included as a random
440 factor to account for variation in intercepts and slopes. Moreover, in the Agrodiversity

experiment, species were planted at different densities in mixture communities[13], enabling tests of whether reversing species-abundance ranks affected the estimation of the covariance effect (Box 1). We calculated correlation coefficients between species abundances and the estimated covariance effects for each plot relative to those in the plot with uniformly high planting densities. Then, we analyzed the relationship between species-abundance and covariance-effect correlation coefficients using a linear mixed-effects model, with site included as a random factor to account for its influence on both intercepts and slopes.

All statistical analyses were conducted in R 4.5.2[50], using the *lme4* package for linear regression, residual regression, and analysis of variance, the *MuMIn* package for estimating marginal R^2 and conditional R^2, and the *DescTools* package for estimating the Gini index. Effects were considered statistically significant if $P < 0.05$.

Data and Code availability

The data and R code generated and/or analyzed in the current study have been deposited in Figshare in accordance with the journal's data availability requirements.

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Author contributions

Y.W. conceived the idea for this research and developed the method for partitioning the average and covariance effects applicable across experimental and natural systems. Y.W. analyzed the data and wrote the paper with contributions from J.W., S.W., B.S., N.E. and Y.H.. N.E. contributed observations from the Jena biodiversity experiment. W.M. initiated the multi-site community survey and nitrogen addition experiment in the Inner Mongolian grasslands, and Y.W., W.M., B.M., B.Z., X.D. and X.J. conducted the community survey in the subsequent years. J.-S.H. initiated the nitrogen addition experiment in the Tibetan alpine grassland, and C.W., Z.Z. and H.L. conducted the observations. B.M. also analyzed the climatic data from the Inner Mongolian grasslands.

Competing interests

The authors declare no competing interests.

Supplementary Information

Supplementary information may be found online at the end of this article.

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Box 1. Partitioning the average and covariance effects

Considering a community containing S species that has reached a stable state, we investigated its temporal changes in ecosystem functioning based on the concept of community temporal stability (*i.e.*, the mean-to-standard-deviation ratio), given its consistent application in both empirical and biodiversity experimental studies[11,22,35]. Accordingly, temporal deviations in community-level ecosystem functioning (*i.e.*, anomalies) were quantified by comparing the community observed at time t with the community averaged across all T observations, here explicitly defined as a "reference community" (Box 1–Figure 1). Theoretical studies[21,36–38] often assume that species fluctuate randomly in abundance over time. Following this assumption, we partitioned temporal deviations in ecosystem functioning into random and non-random components, which can be described using the variables defined below.

$Y_O(i, t)$: number of individuals (or yield, productivity and coverage) of species i in observation t, with total community value given by $Y_O^{total}(t) = \Sigma_i Y_O(i, t)$

$Y_R(i) = \Sigma_t Y_O(i, t) / T$: mean abundance (or yield, productivity and coverage) of species i in the reference community, with the total value across all S species given by $Y_R^{total} = \Sigma_i Y_R(i)$ and the mean abundance across all S species given by $\overline{Y_R} = \Sigma_i Y_R(i) / S$

$RC(i, t) = (Y_O(i, t) - Y_R(i)) / Y_R(i)$: relative change in species i at observation t relative to $Y_R(i)$, with mean relative change across species given by $\overline{RC(t)} = \Sigma_i RC(i, t) / S$

$\Delta Y^{total}(t) = Y_O^{total}(t) - Y_R^{total} = \Sigma_i Y_O(i, t) - \Sigma_i Y_R(i)$: temporal deviation between the community at time t and the reference community (*i.e.*, anomaly). The temporal standard deviation estimated from $\Delta Y^{total}(t)$ is identical to that estimated directly from $Y_O^{total}(t)$

628

629 Then, $\Delta Y^{total}(t)$ can be described as follows:

630 $$\Delta Y^{total}(t) = \sum_i (RC(i,t)+1)Y_R(i) - \sum_i Y_R(i) = S\overline{RC(t)}\,\overline{Y_R} + S\,cov(RC(t), Y_R), \quad (1)$$

631 Following the multi-scale temporal stability framework[49], we further extended this
632 formulation to account for temporally and spatially repeated surveys. Let $Y_O(t, p)$ represent the
633 community observed at time t within plot p, the corresponding deviation from the reference
634 community (where $Y_R(i) = \Sigma_t\Sigma_p Y_O(i, t, p) / (TP)$ for species i) is then given by:

635 $$\Delta Y^{total}(t,p) = S\,\overline{RC(t,p)}\,\overline{Y_R} + S\,cov(RC(t,p), Y_R), \quad (2)$$

636 The average and covariance terms on the right-hand side of Equations (1) and (2) can be
637 intuitively interpreted by analogy to the endemic-area relationship[39]. When individuals are
638 randomly distributed, or equivalently when species are treated identically as in the neutral
639 model[40], reducing an intact habitat from area a to a subset area a' causes all species to lose
640 individuals in equal proportions (*i.e.*, $RC(i, t) = \overline{RC(t)}$). Under this scenario (Case 1 in Box 1–
641 Figure 1), the average effect alone captures changes in total abundance and the associated
642 probabilities of species occurrence, and thus determines the observed species richness within the
643 subset area[39], whereas species composition remains unchanged, as indicated by a zero covariance
644 effect. In contrast, non-random spatial distributions cause disproportionate losses among
645 species[39], resulting in compositional changes and a non-zero covariance effect. A positive
646 covariance effect arises when species with above-average abundances in the reference
647 community tend to exhibit above-average relative changes, whereas species with below-average
648 abundances tend to exhibit below-average relative changes. As a result, already abundant species
649 become increasingly dominant and subordinate species become rarer, resulting in greater

abundance unevenness and reduced species richness. Conversely, a negative covariance effect produces the opposite pattern (Case 2 in Box 1–Figure 1).

Based on Equation (1), we can describe the covariance effect as follows:

$$S\,cov(RC(t), Y_R) = \sum_i (RC(i,t) - \overline{RC(t)})(Y_R(i) - \overline{Y_R}) = \sum_i (RC(i,t) - \overline{RC(t)})Y_R(i), \quad (3)$$

Equation (3) indicates that the covariance effect is weighted by species abundances in the reference community ($Y_R(i)$) and is therefore disproportionately influenced by high-abundance species, unlike the average effect, which weights all species equally. To verify this disproportionate contribution, we separated both the average and covariance effects into dominant and subordinate species groups. This is achieved by introducing two complementary Boolean vectors to label if species i is a dominant species ($D(i) = 1$, otherwise 0) or a subordinate species ($U(i) = 1$, otherwise 0), respectively. The average and covariance effects can thereby be described as follows:

$$S\overline{RC(t)}\,\overline{Y_R} = S\sum_i \frac{RC(i,t)}{S}\sum_i \frac{Y_R(i)}{S} = S\sum_i \frac{D(i)RC(i,t)+U(i)RC(i,t)}{S}\sum_i \frac{D(i)Y_R(i)+U(i)Y_R(i)}{S}$$

$$= S\sum_i \frac{D(i)RC(i,t)}{S}\sum_i \frac{D(i)Y_R(i)}{S} + S\sum_i \frac{U(i)RC(i,t)}{S}\sum_i \frac{U(i)Y_R(i)}{S} + S\sum_i \frac{D(i)RC(i,t)}{S}\sum_i \frac{U(i)Y_R(i)}{S} +$$

$$S\sum_i \frac{U(i)RC(i,t)}{S}\sum_i \frac{D(i)Y_R(i)}{S}, \quad (4)$$

$$S\,cov(RC(t), Y_R) = \sum_i D(i)\big(RC(i,t) - \overline{RC(t)}\big)(Y_R(i) - \overline{Y_R}) + \sum_i U(i)\big(RC(i,t) -$$

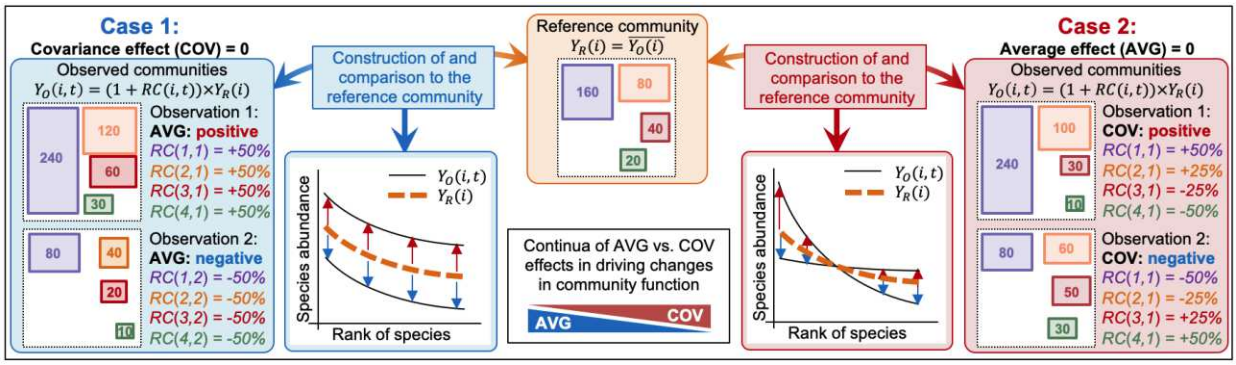
$$\overline{RC(t)}\big)(Y_R(i) - \overline{Y_R}), \quad (5)$$

where the first two terms on the right-hand side of Equation (4) and the two terms on the right-hand side of Equation (5) are defined as dominant-species and subordinate-species components of the average and covariance effects, respectively, because they are driven exclusively by dominant or subordinate species.

Considering the correlation coefficient, $\rho_t = cov(RC(t), Y_R)/\sqrt{var(RC(t))var(Y_R)}$, between species relative changes in observation *t* and species abundances in the reference community, Equation (1) can be rewritten as:

$$\Delta Y^{total}(t) = S\overline{RC(t)}\,\overline{Y_R} + S\rho_t\sqrt{var(RC(t))var(Y_R)}, \quad (6)$$

where the two terms on the right-hand side of Equation (6) are the average and covariance effects, respectively, providing more intuitive insights into the impacts arising solely from changes in species abundances within the reference community and from controlling species abundances in biodiversity experiments[12–14]. For the average effect, controlling species abundances alters the mean of species abundances and produces well-linearly correlated estimations. In contrast, the covariance effect is jointly affected by the abundance-dependent response of species (ρ_t) and the variance of species abundances ($var(Y_R)$), both of which can be altered by controlling species abundances[12–14], making the estimation of the covariance effect more sensitive to changes in species-abundance distributions than that of the average effect. When species-abundance ranks are reversed, as in the design of the Agrodiversity experiment[13], the sign of ρ_t and consequently the sign of the estimated covariance effect can also be reversed. Furthermore, this description indicates that high unevenness and correspondingly high variance of species abundances do not necessarily indicate a strong covariance effect. However, when species with above-average performance ultimately attain higher-than-average abundances, this performance-associated dominance pattern can generate a strong covariance effect.



Box 1–Figure 1. Conceptual model of temporal changes in ecosystem functioning and the associated average and covariance effects. Building on the concept of community temporal stability, these effects are quantified by comparing the observed communities at time *t* with the community averaged across all *T* observations, explicitly represented by the reference community. Two extreme cases are illustrated, one in which temporal changes in ecosystem functioning arise solely from the average effect (Case 1) and another in which they arise solely from the covariance effect (Case 2).

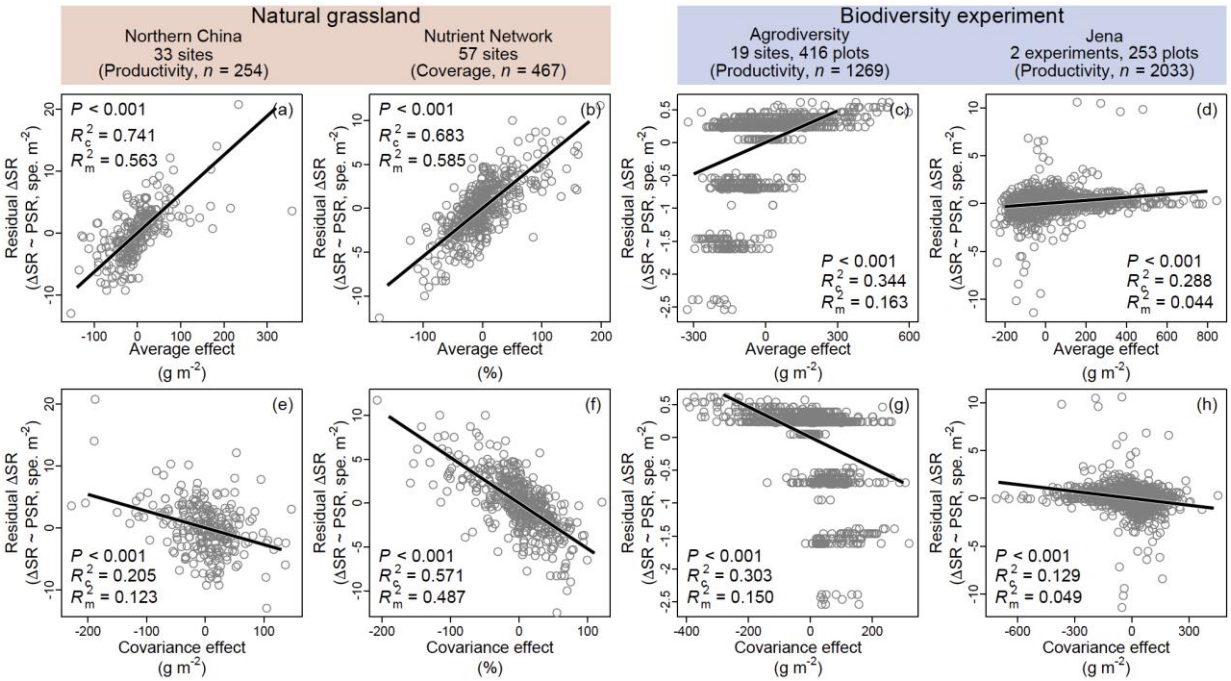


Figure 1. Species richness in relation to the average and covariance effects. Shown are relationships of residual changes in species richness (Extended Data Figure 1a–d) with the average (a–d) and covariance (e–h) effects for both natural grasslands (a–b and e–f) and biodiversity experiments (c–d and g–h). Solid black lines represent significant regression lines, with conditional and marginal R^2 values (R_c^2 and R_m^2) shown in the figures (details for the main and dominance experiments in Jena are provided in Extended Data Figure 2–3).

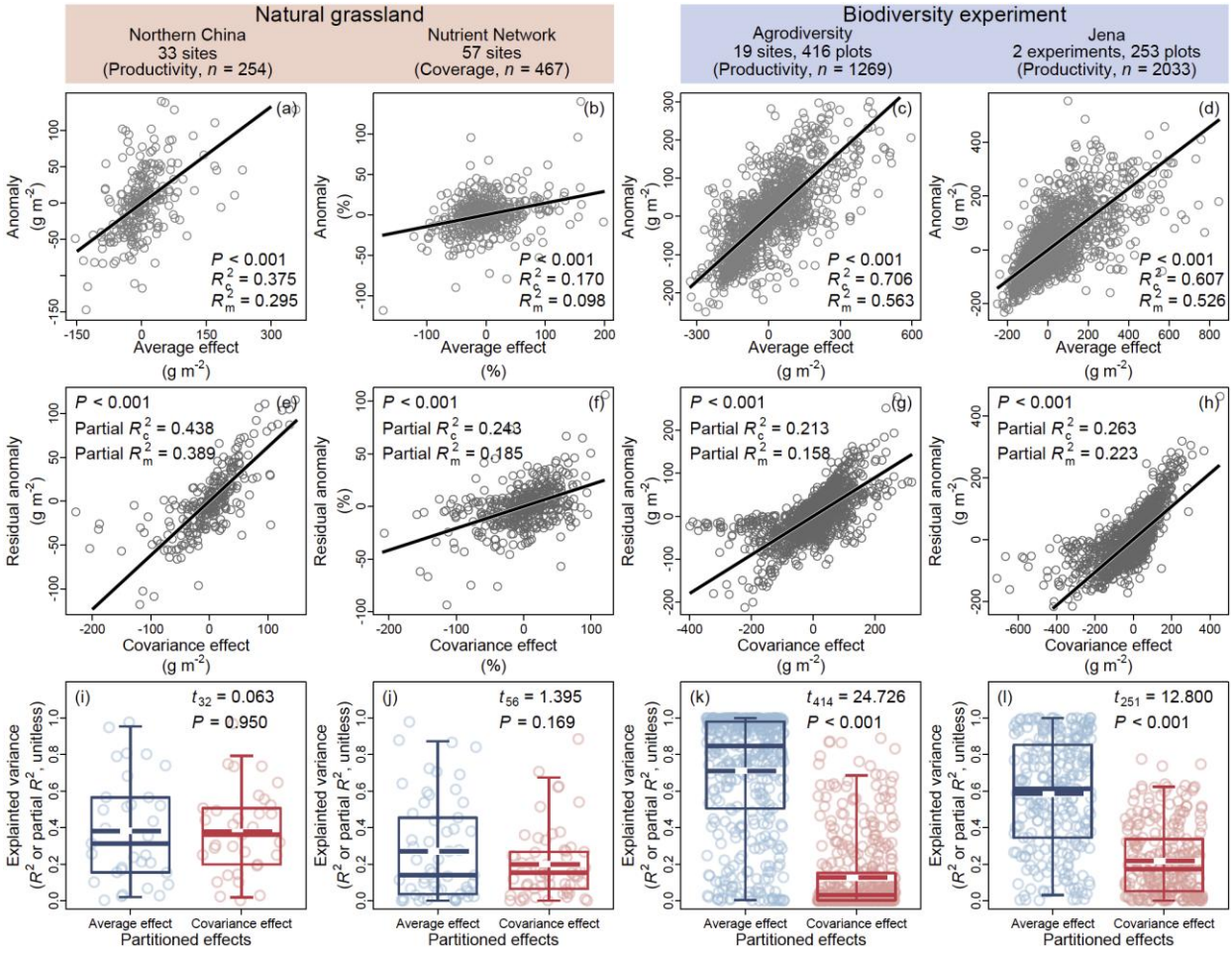


Figure 2. Average and covariance effects in driving ecosystem functioning. Relationships between temporal deviations in ecosystem functioning (*i.e.*, anomalies) and the average effect (a–d), and between their residuals and the covariance effect (e–h), are shown for both natural grasslands (a–b, e–f and i–j) and biodiversity experiments (c–d, g–h and k–l). Conditional and marginal R^2 (R_c^2 and R_m^2) from linear regressions, and partial R_c^2 and R_m^2 from residual regressions, are reported for the average and covariance effects, respectively. Solid black lines represent significant relationships. The contributions of the two effects to ecosystem functioning (i–j; see Extended Data Figure 4 for the main and dominance experiments in Jena) were compared (using paired *t*-tests). Boxes (i–l) show medians (solid lines), means (dashed lines), interquartile ranges (boxes) and the 2.5th and 97.5th percentiles (whiskers).

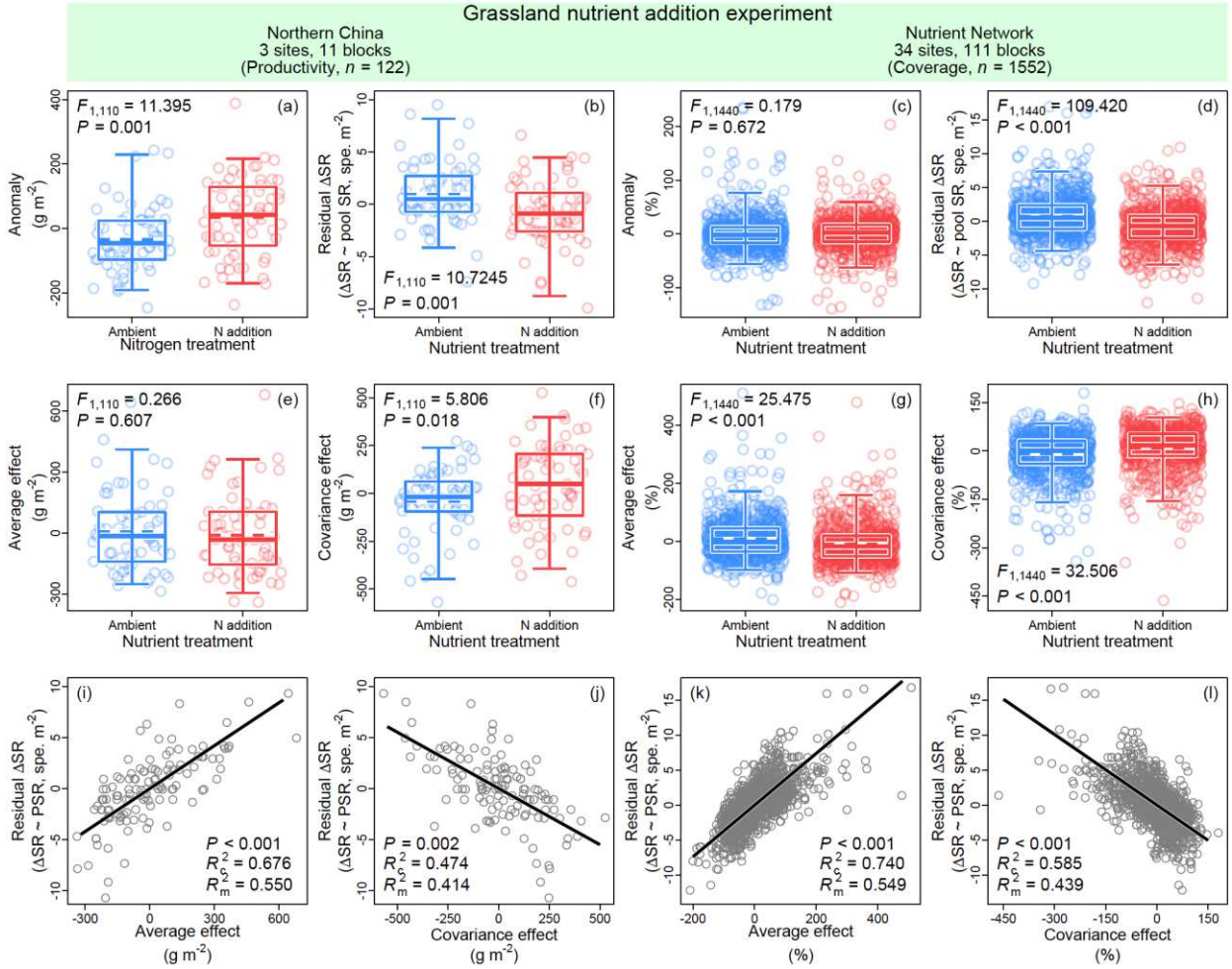


Figure 3. Effects of nitrogen addition on plant community. Shown are the effects (*F*-values) of nitrogen addition on ecosystem functioning (a and c), residual changes in species richness (b and d; Extended Data Figure 5a–b), the average (e and g) and covariance (g and h) effects, as well as relationships of residual changes in species richness with the average (i and k) and covariance (j and l) effects for both northern China grasslands (a–b, e–f and i–j) and Nutrient-Network grasslands (c–d, g–h and k–l). Boxes (a–h) show medians (solid lines), means (dashed lines), interquartile ranges (boxes) and the 2.5th and 97.5th percentiles (whiskers). Solid black lines represent significant regression lines, with conditional and marginal R^2 values (R_c^2 and R_m^2) shown in the figures.

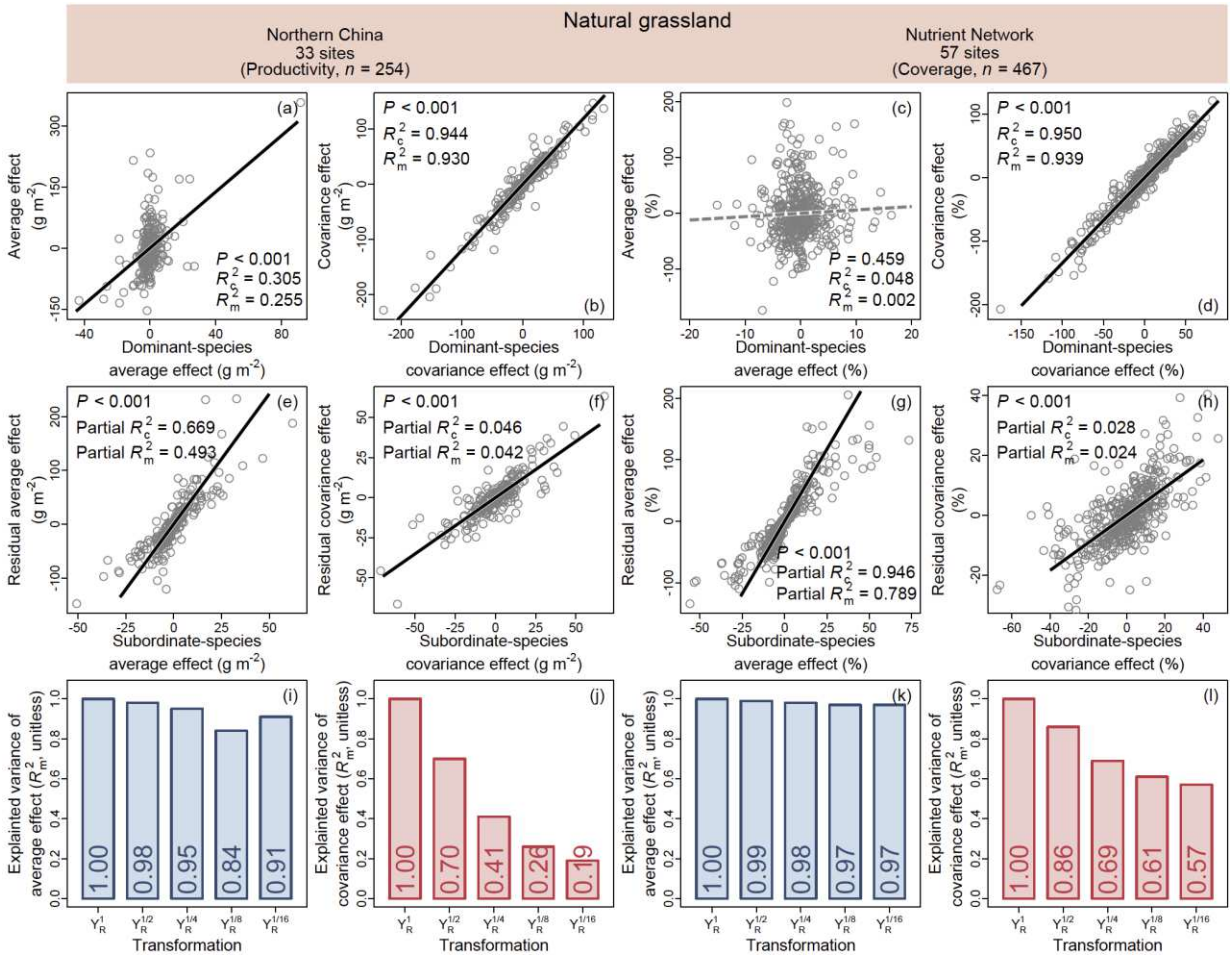


Figure 4. Driving forces of the average and covariance effects. Average (a, c, e and g) and covariance (b, d, f and h) effects in relation to their dominant-species (a–d) and subordinate-species (e–h) components, as well as the effects of altered species-abundance unevenness (i–l) on the average and covariance effects. Solid black and dashed grey lines represent significant and non-significant regression lines (a–h), respectively. Conditional and marginal R^2 (R_c^2 and R_m^2) values from linear regressions are shown for the dominant-species components (a–d), whereas partial R_c^2 and R_m^2 from residual regressions (e–h) are shown for the subordinate-species components (e–h).

Supplementary Files

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