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Although numerous studies have demonstrated a positive relationship between biodiversity and ecosystem stability, that is low temporal variability in ecosystem functions, the role of interspecific interactions in driving this relationship remains elusive. Here we develop a partitioning framework to disentangle the effects of interspecific interactions on ecosystem variability from those of interaction-independent processes. Applying this framework to competition models and biodiversity experiments in European and North American grasslands, we find that species-specific dynamics observable in monocultures (for example, environmental responses or demographic stochasticity), rather than interspecific interactions observable only in mixtures, explain much of the stabilizing effects of biodiversity on ecosystems. The weak net effect of interspecific interactions results from two counter-balancing effects: an interaction-driven increase in average species variability and an interaction-driven decrease in average species synchrony. We also find that interspecific interactions contributing to higher ecosystem functioning tend to reduce ecosystem variability. Our study provides a systematic empirical assessment of the role of interspecific interactions in shaping grassland ecosystem stability, challenging traditional assumptions about their importance and highlighting species-specific dynamics as the primary mechanism underlying the pervasive biodiversity–stability relationship.

Accelerating environmental and biodiversity changes pose substantial challenges to the stability of ecosystems and the essential services they provide. Ecosystem stability is commonly evaluated by measuring the temporal variability of certain ecosystem functions, typically quantified using the coefficient of variation (CV)—the ratio of the standard deviation to the mean[1]. The temporal variability of ecosystems is jointly determined by the average magnitude of species fluctuations (species variability) and the synchrony among species (species synchrony)[2]. Numerous theoretical and experimental studies have shown that species diversity can stabilize ecosystem temporal dynamics via decreasing species synchrony[3–6], because a decrease in the functional contribution of one species is compensated by an increase in that of other species[7,8]. In ecological communities, asynchronous species fluctuations may arise from species-specific responses to environmental and demographic stochasticity, and/or compensatory dynamics driven by interspecific interactions, such as competition[9,10].

The role of interspecific interactions in stabilizing ecosystem functioning has long been illustrated by theoretical studies. In competitive communities, competition could promote compensatory dynamics among species, thus potentially stabilizing ecosystem properties[11].
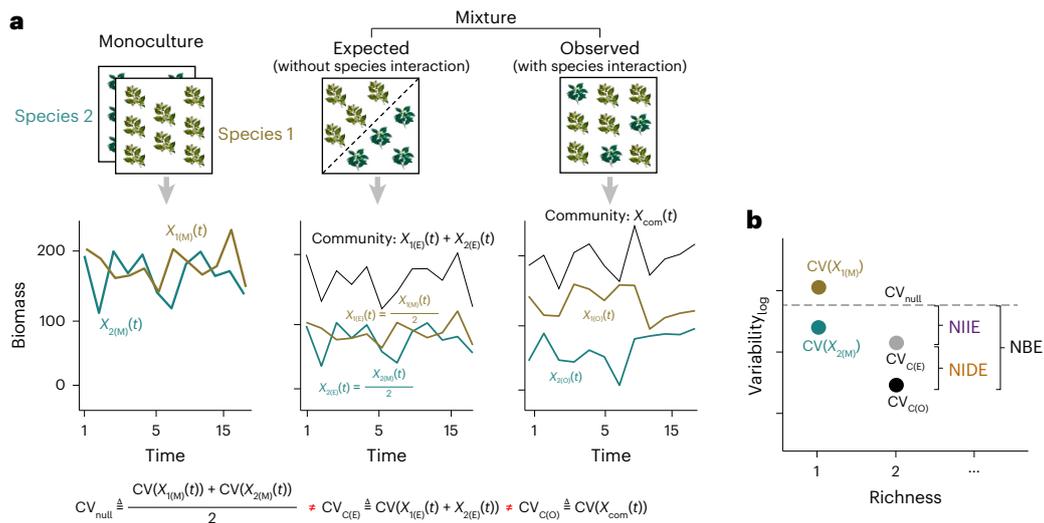
Fig. 1 | A conceptual graph illustrates the interaction-independent and interaction-dependent effects of biodiversity on community variability. **a**, We define NBE_{cv} as the ratio between the $CV_{C(O)}$ and a statistical baseline defined by the average of monoculture variability (CV_{null}), that is, $NBE_{CV} = CV_{C(O)}/CV_{null}$. We then define an ecological baseline ($CV_{C(E)}$) to represent the variability of a hypothetical community consisting of non-interacting species that exhibit the same variability and synchrony as their respective monocultures. **b**, The NBE_{cv} can be partitioned multiplicatively into $NIIE = CV_{C(E)}/CV_{null}$ and $NIDE = CV_{C(O)}/CV_{C(E)}$. Or equivalently, an additive partition holds on log scales: $\log(NBE_{CV}) = \log(NIIE) + \log(NIDE)$. The dotted grey line represents the statistical baseline (CV_{null}).

However, dynamic community models have shown that while decreasing species synchrony, competition also tends to increase species variability[2,9]. In symmetric models with identical interaction strengths, these two effects cancel each other out completely, such that competition has no effect on community variability[9,12]. In cases with asymmetric competition, these two effects cancel out only partially, resulting in a positive or a negative net effect on community variability[9,13]. Therefore, in realistic communities where species interactions are typically asymmetric[14–16], competition may have either net stabilizing or destabilizing effects. Despite these theoretical insights, the effects of interspecific interactions have yet to be addressed quantitatively in empirical studies, largely due to the lack of a theoretical framework separating the effects of interspecific interactions from interaction-independent processes; for example, species-specific environmental responses or demographic stochasticity (but see ref. 17).

Biodiversity experiments provide a useful platform to quantify the effects of species interactions on ecosystem functioning and stability. In particular, ref. 18 developed an additive partitioning approach to disentangle the effects of biodiversity on ecosystem functioning using experimental data. By comparing the observed value of mixture productivity to that expected from a hypothetical community with non-interacting species, this framework quantifies a net biodiversity effect and partitions it into two ecological processes: the complementarity effect, arising from niche differentiation or positive interactions among species; and the selection effect, arising from the dominance of species with higher or lower productivity[18,19]. The key to this framework is the construction of a hypothetical non-interacting community based on monocultures, which serves as a baseline to determine the effects of interspecific interactions on productivity. Despite the simultaneous development of biodiversity–ecosystem functioning and biodiversity–ecosystem stability research[20,21], particularly since the 2000s, an analogous framework to assess the effects of species interactions on ecosystem stability is still missing.

Here we develop a theoretical framework to partition the effects of biodiversity on community variability into two main components: interaction-dependent and interaction-independent effects. This partitioning is achieved by comparing the observed variability of ecosystem functioning in mixtures with that expected from monocultures, which requires data of species-level functions in both mixtures and monocultures (for example, biodiversity experiments[3,22]). Akin to the partitioning framework of ref. 18, our framework further partitions the interaction-dependent effects into average effects of interspecific interactions on species variability or species synchrony, and selection effects of interspecific interactions that lead to the dominance of certain species whose variability or synchrony is greater or less than that of other species. This framework allows not only to disentangle the multiple processes through which biodiversity contribute to ecosystem stability, but also understand how these processes are associated with those underlying biodiversity effects on ecosystem functioning (that is, complementary and selection effects[18]).

We then apply this framework to a competition model and a dataset of 34 grassland biodiversity experiments to quantify the multiple processes underlying biodiversity–ecosystem stability relationships and investigate their associations with processes driving biodiversity–ecosystem functioning relationships. Previous studies using these experiments have demonstrated the stabilizing effects of biodiversity, that is, lower ecosystem variability in more diverse communities[3,23]. However, whether interspecific interactions or interaction-independent processes contribute to these stabilizing effects remains unexplored. Our results shed new light on a long-standing debate on the causes of widely observed positive diversity–stability relationships, which we find are predominantly due to variation in species-specific dynamics rather than interspecific interactions.

Results

A framework to partition the stabilizing effects of biodiversity
The typical approach to examining both biodiversity–ecosystem functioning and biodiversity–ecosystem stability relationships is to fit a linear regression, on natural or log scales, between an ecosystem function or its temporal variability and species richness. With this approach, an implicit null hypothesis is that the observed ecosystem function or variability equals the average of monoculture functioning or variability across constituent species, which serves as a statistical baseline (Fig. 1a). Any deviation from this statistical baseline (that is, a non-zero regression slope) indicates a positive or negative biodiversity effect[6,18,24]. In biodiversity–ecosystem functioning studies, this statistical baseline has
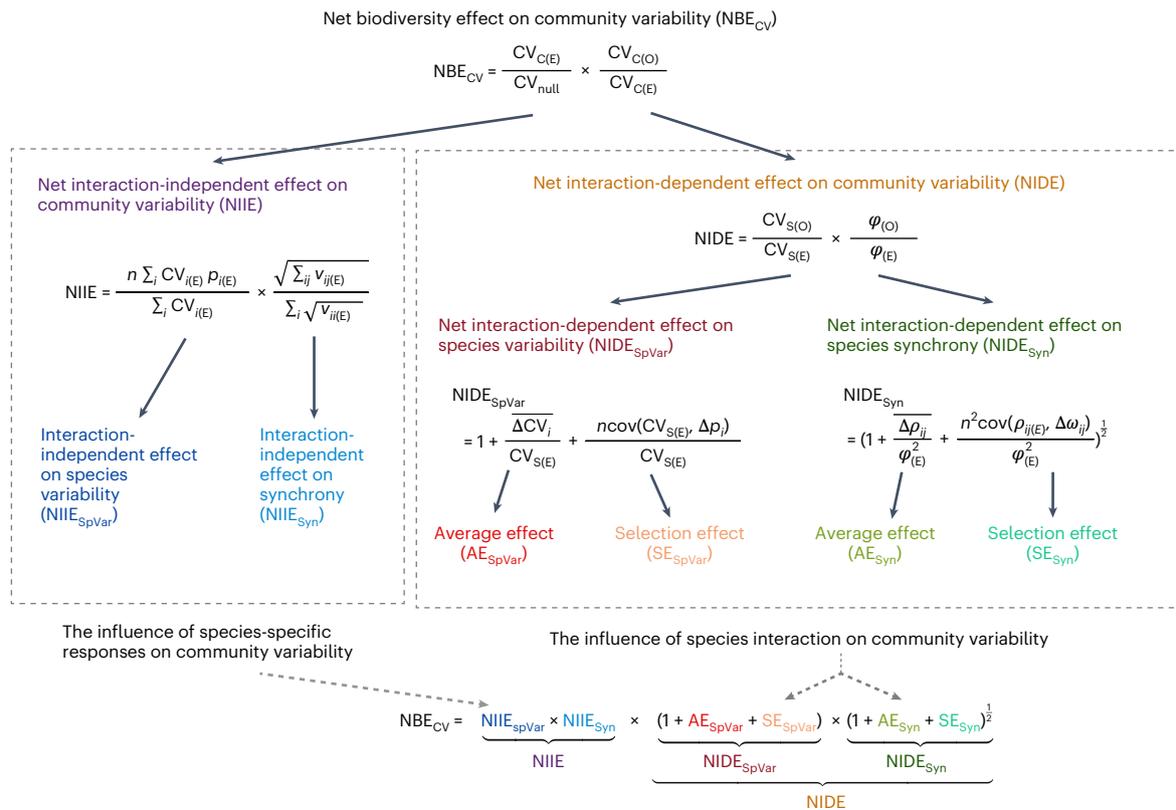
Fig. 2 | A partitioning framework for disentangling the mechanisms underlying NBE$_{CV}$. NIIE can be partitioned multiplicatively into two components: NIIE$_{SpVar}$ and NIIE$_{Syn}$. NIDE arises from four interaction-mediated pathways: AE$_{SpVar}$, AE$_{Syn}$, SE$_{SpVar}$ and SE$_{Syn}$. Detailed definitions in Methods.

a clear ecological underpinning: the ecosystem function (for example, productivity) of a mixture composed of multiple non-interacting species in equal proportions is equal to the average of the monoculture functions[18]. However, in biodiversity–ecosystem stability studies, the temporal variability of a mixture composed of multiple non-interacting species in equal proportions (referred to as the ecological baseline, CV$_{C(E)}$) is not equal to the average of monoculture variability[25] (referred to as the statistical baseline, CV$_{null}$; Fig. 1a). Indeed, CV$_{C(E)}$ is usually lower than CV$_{null}$ because of asynchronous fluctuations among monocultures, and they are identical only when all monocultures were perfectly synchronous and equally abundant (Supplementary Appendix 1). The difference between the statistical baseline (CV$_{null}$) and the ecological baseline (CV$_{C(E)}$) is largely overlooked in biodiversity–ecosystem stability studies. As a result, interpretations of biodiversity–stability relationships often invoke a mixture of possible mechanisms (that is, interaction-dependent and interaction-independent effects)[26–28].

By comparing the observed community variability (CV$_{C(O)}$), the ecological baseline (CV$_{C(E)}$) and the statistical baseline (CV$_{null}$), it becomes possible to disentangle two groups of mechanisms underlying the stabilizing effects of biodiversity (Fig. 1b). We define the net biodiversity effect on community variability (NBE$_{CV}$) as the ratio between CV$_{C(O)}$ and the average variability of monocultures CV$_{null}$. We then partition NBE$_{CV}$ into two components:

$$\text{NBE}_{CV} = \frac{CV_{C(O)}}{CV_{null}} = \underbrace{\frac{CV_{C(E)}}{CV_{null}}}_{\text{NIIE}} \times \underbrace{\frac{CV_{C(O)}}{CV_{C(E)}}}_{\text{NIDE}} \qquad (1)$$

The first component represents the net interaction-independent effect on community variability (NIIE), calculated as the ratio between CV$_{C(E)}$ and CV$_{null}$. NIIE quantifies how the variability of a hypothetical community consisting of multiple non-interacting species differs from the simple average of monoculture variability. The second component

represents the net interaction-dependent effect on community variability (NIDE), defined as the ratio between CV$_{C(O)}$ and CV$_{C(E)}$. NIDE captures the net effects of interspecific interactions on community variability, mediated by changes in the magnitude and synchrony of species fluctuations (Fig. 1). NIIE and NIDE could be further partitioned to uncover the various processes underlying biodiversity–stability relationships (Fig. 2). Below we provide intuitive explanations of the rationale of the partition, and we refer the readers to Methods for more detailed explanations and to Supplementary Information for complete derivation.

NIIE can further be partitioned into two components (Fig. 2a and Methods):

$$\text{NIIE} = \text{NIIE}_{SpVar} \times \text{NIIE}_{Syn} \qquad (2)$$

The first component captures the net interaction-independent effect on species variability (NIIE$_{SpVar}$), which arises if the expected community is dominated by species with high or low monoculture variability. This effect depends on the function distribution among monocultures as well as on the correlation between the mean and variance of functions across monocultures (for example, Taylor's law)[11,29]. The second component captures the degree of synchrony among monocultures (NIIE$_{Syn}$) arising from interaction-independent processes such as species-specific environmental responses, demographic stochasticity and so on[7,17]. Conceptually, NIIE$_{Syn}$ corresponds to the portfolio effect or the buffering effect in the literature[11,30,31].

NIDE can be further partitioned as follows (Fig. 2b and Methods):

$$\text{NIDE} = \underbrace{\left(1 + AE_{SpVar} + SE_{SpVar}\right)}_{\text{NIDE}_{SpVar}} \times \underbrace{\left(1 + AE_{Syn} + SE_{Syn}\right)^{\frac{1}{2}}}_{\text{NIDE}_{Syn}} \qquad (3)$$

Equation (3) identifies four ways in which interspecific interactions can influence community variability: (1) by changing the average
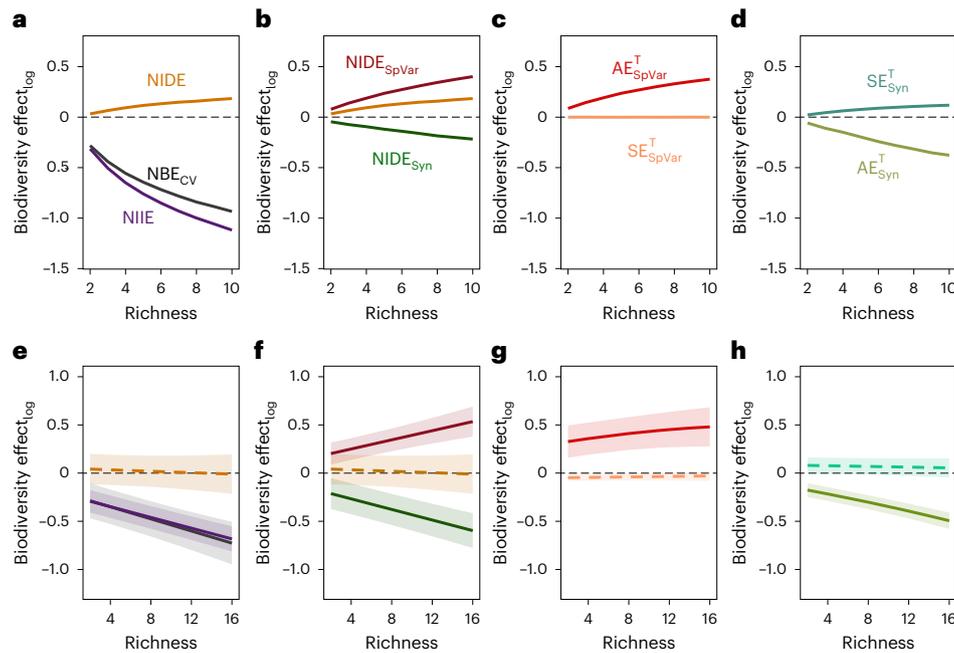
Fig. 3 | NBE_{CV} and its multiple components as functions of species richness. **a**–**h**, Results are shown for model ecosystems (**a**–**d**) and grassland experiments (**e**–**h**). **a**,**e**, NBE_{CV} (**a**) and its two components (**e**) on log scales: $\log(NBE_{CV}) = \log(NIIE) + \log(NIDE)$. **b**,**f**, The two components of NIDE on log scales: $\log(NIDE) = \log(NIDE_{SpVar}) + \log(NIDE_{Syn})$. **c**,**g**, The two components of $NIDE_{SpVar}$ in approximated terms: $\log(NIDE_{SpVar}) \approx AE^T_{SpVar} + SE^T_{SpVar}$. **d**,**h**, The two components of $NIDE_{Syn}$ in approximated terms: $\log(NIDE_{Syn}) \approx AE^T_{Syn} + SE^T_{Syn}$. See text for definitions of notations and Methods for definitions of AE^T_{SpVar}, SE^T_{SpVar}, AE^T_{Syn} and SE^T_{Syn}. In **a**–**d**, coloured lines represent least-square fits across

10,000 communities generated from Lotka–Volterra competition models. Parameters are $\alpha_{ij} = U(0.01,0.41)$, $\log_2(r) \sim U(-1,0)$, $\log_2(K) \sim U(-1,0)$, $\mu_{e,i} = 0.2$, $\mu_{d,i} = 0$ and $\sigma_{e,i} = U(0.0,0.1)$. In **e**–**h**, coloured lines with error bands represent the overall fits and 95% confidence intervals from linear mixed-effects models across grassland experiments. Solid lines show significant relationships with species richness ($P < 0.05$); dashed lines show non-significant relationships. Relationships within each experiment are shown in Supplementary Fig. 1 and detailed statistical results are provided in Supplementary Tables 2–4.

magnitude of species variability, which we call the average effect of interactions on species variability (AE_{SpVar}); (2) by selecting species with greater/smaller variability, which we call the selection effect of interactions on species variability (SE_{SpVar}); (3) by changing the average synchrony in biomass fluctuations across species pairs, which we call the average effect of interactions on species synchrony (AE_{Syn}); and (4) by selecting species pairs with more/less synchronous dynamics, which we call the selection effect of interactions on species synchrony (SE_{Syn}). For both species variability and synchrony, the average and selection effects quantify the interaction-induced proportional changes, which are parallel to normalized forms of complementarity and selection effects from the classic additive partition in biodiversity–ecosystem functioning relationship[18] (Methods).

Partitioning biodiversity effects in model communities
To illustrate the multiple pathways through which biodiversity affects community variability (Fig. 2), we investigate a Lotka–Volterra model in which population dynamics are governed by competition and environmental stochasticity (Methods). Across simulated communities with randomly assigned parameter values, greater species diversity contributes to decreasing community variability (Fig. 3a). This net stabilizing effect of diversity is mainly due to NIIE, whereas NIDE is weak (Fig. 3a). Interspecific interactions (that is, competition in this model) increase the average population variability (positive AE_{SpVar}) while decreasing the average species synchrony (negative AE_{Syn}; Fig. 3c,d and Extended Data Fig. 1); these two effects act in opposite directions, resulting in a weak net effect on community variability (NIDE; Fig. 3 and Extended Data Fig. 1). In addition, competition generates weak selection effects on species variability and moderate selection effects on species synchrony by increasing species unevenness (Fig. 3c,d and Extended Data Fig. 1). In the extreme case where parameters of species dynamics

and interactions are identical, our analytic solutions show that the positive AE_{SpVar} and negative AE_{Syn} cancel out perfectly, and the selection effects are zero ($SE_{SpVar} = SE_{Syn} = 0$), regardless of the strength of competition or the number of species (Methods). This result confirms previous theoretical studies showing that competition should have no effect on the variability of symmetric communities with identical parameters[12,13].

While competition exhibits weak selection effects in randomly assembled communities, it can have more pronounced effects on community variability when species dynamical parameters co-vary or exhibit trade-offs. When the intrinsic growth rate of species correlates negatively with their carrying capacities (r–K trade-off) or positively with the overall strength of competition from other species (growth-competition trade-off), communities will be dominated by species with higher species variability, leading to a positive SE_{SpVar} (Extended Data Fig. 2a). In contrast, if the intrinsic growth rate correlates positively with the carrying capacity, competition will select less variable species and lead to a negative SE_{SpVar} (Extended Data Fig. 2c). In addition, in the presence of demographic stochasticity, competition tends to decrease the mean of community function and thus increase community variability (but see ref. 13), even under symmetric competition (Methods).

Our models also predict associations between the effects of interspecific interactions on community variability (AE_{SpVar}, AE_{Syn}, SE_{SpVar} and SE_{Syn}) and those on community biomass, that is, the complementarity effects (CE'_{Bio}) and selection effects (SE'_{Bio}) derived from the additive partition of biodiversity–ecosystem functioning relationship[18]. For a given level of species richness, the absolute magnitude of both AE_{Syn} and AE_{SpVar} increases, while that of CE'_{Bio} decreases, as competition strength increases (Extended Data Fig. 1). As a result, CE'_{Bio} and AE_{SpVar} are negatively associated and CE'_{Bio} and AE_{Syn} are positively
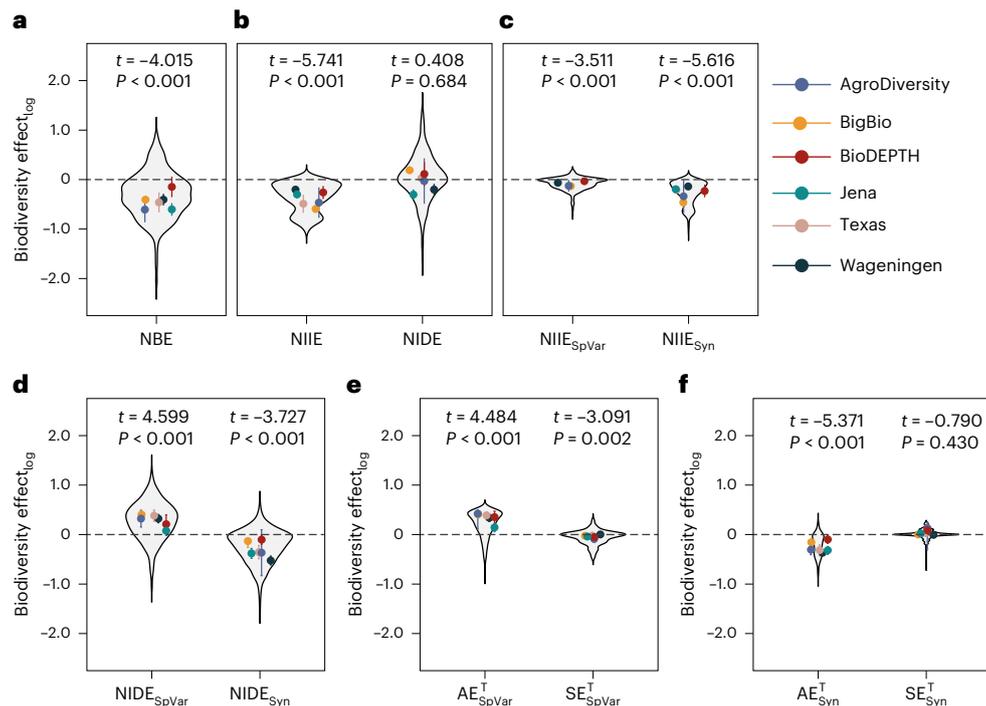
Fig. 4 | NBE$_{CV}$ and its multiple components across 34 grassland biodiversity experiments. a–f, Biodiversity effects in experiments conducted across North America and Europe are shown for NBE$_{CV}$ (**a**), NIIE and NIDE (**b**), NIIE$_{SpVar}$ and NIIE$_{Syn}$ (**c**), NIDE$_{SpVar}$ and NIDE$_{Syn}$ (**d**), AE$^T_{SpVar}$ and SE$^T_{SpVar}$ (**e**), and AE$^T_{Syn}$ and SE$^T_{Syn}$ (**f**). All components are log-transformed, except for AE$^T_{SpVar}$, SE$^T_{SpVar}$, AE$^T_{Syn}$ and SE$^T_{Syn}$

(Methods). The violin shows the overall distribution within the 99th percentile across biodiversity experiments. The coloured scatter represents the specific component within each biodiversity experiment; the error bar is 95% confidence interval. The sample size (n) is 447. Two-sided t-tests were used to assess whether the effect size differed from zero in linear mixed-effects models (d.f. = 430).

associated (note that AE$_{Syn}$ is generally negative), along a gradient of competition strength (Extended Data Fig. 3a,e). However, as species richness increases, the absolute magnitudes of AE$_{Syn}$, AE$_{SpVar}$ and CE'$_{Bio}$ all tend to increase, resulting in a positive association between CE'$_{Bio}$ and AE$_{SpVar}$ and a negative association between CE'$_{Bio}$ and AE$_{Syn}$ along a gradient of species richness (Extended Data Fig. 3a,e). In addition, in the presence of demographic stochasticity, SE'$_{Bio}$ tends to correlate positively with SE$_{Syn}$ (Extended Data Fig. 3d,h), but negatively with SE$_{SpVar}$ (Extended Data Fig. 3g). Overall, stronger biodiversity effects on community biomass (more positive NBE'$_{Bio}$) are associated with stronger net interaction-dependent effects on community variability (more negative NIDE), especially in the presence of demographic stochasticity (Extended Data Fig. 4).

Partitioning biodiversity effects in grassland experiments

We now apply our partitioning framework to multiple datasets of grassland biodiversity experiments to quantify the relative contributions of the multiple pathways by which biodiversity affects ecosystem variability under field conditions. Our dataset includes 34 experimental sites across North America and Europe (Extended Data Fig. 5). Using these experiments, previous studies have documented negative relationships between species diversity and community variability[3,23]. Below we illustrate the contributions of interaction-independent and interaction-dependent processes to the stabilizing effects of biodiversity.

Our analysis of these experiments reveals patterns highly consistent with those from simulated communities (Fig. 3). Specifically, we found that the negative relationship between species richness and ecosystem variability was driven mainly by NIIE, whereas NIDE was weak and distributed around zero (Fig. 4). NIIE was negative and decreased as species richness increased across different experiments, contributing to the stabilization of community biomass (Fig. 3a). These stabilizing effects arose from interaction-independent asynchrony among species and a negative interaction-independent effect on average species variability, especially at higher levels of species richness (Fig. 4c and Supplementary Fig. 1d,e). In comparison, NIDE was consistently weak across levels of species richness (Fig. 3e). Interspecific interactions increased AE$_{SpVar}$ (0.476 ± 0.09, t = 5.277, P < 0.001) while decreasing AE$_{Syn}$ (−0.388 ± 0.07, t = −5.111, P < 0.001) (Fig. 4e,f and Supplementary Fig. 3). In addition, interspecific interactions exhibited negative, although weak SE$_{SpVar}$ (−0.043 ± 0.02, t = −2.424, P = 0.016) but non-significant SE$_{Syn}$ (0.165 ± 0.09, t = 1.745, P = 0.082). This suggests that mixtures tended to be dominated by more stable species (those with lower monoculture variability). As species richness increased, the magnitudes of AE$_{SpVar}$ (slope is 0.028, 95% CI [0.016, 0.039], marginal R^2 = 0.036) and AE$_{Syn}$ (slope is −0.030, 95% CI [−0.039, −0.020], marginal R^2 = 0.078; Fig. 3f) both increased. However, these two effects were always of a similar magnitude and thus cancelled each other out, resulting in almost no net effect of interspecific interactions on community variability (Fig. 3). Given the weak net effect of interspecific interactions, the CV$_{C(O)}$ could be well predicted by monoculture dynamics (marginal R^2 = 0.364, conditional R^2 = 0.601; Fig. 5).

Furthermore, NIDE was negatively associated with the net diversity effect on community biomass (slope is −0.087, 95% CI [−0.15, −0.03], marginal R^2 = 0.015; Fig. 6a). The CE'$_{Bio}$ exhibited weak negative correlations with AE$_{SpVar}$ (slope is −0.031, 95% CI [−0.07, 0.01], marginal R^2 = 0.007; Fig. 6b), particularly in the BigBio experiment (slope is −0.06, 95% CI [−0.09, −0.03], marginal R^2 = 0.120) and the Agrodiversity experiment (slope is −0.523, 95% CI [−1.02, −0.02], marginal R^2 = 0.180; Fig. 6b). The SE'$_{Bio}$ was negatively correlated with SE$_{SpVar}$, whether across or within experiments (Fig. 6c) and SE'$_{Bio}$ was positively correlated with SE$_{Syn}$ (slope is 0.053, 95% CI [−0.00, 0.11], marginal R^2 = 0.006; Fig. 6e). Overall, the greater the effects of interspecific interactions in promoting community biomass, the greater they contribute to reducing community variability. In other words, interspecific interactions tend to simultaneously increase the mean and stability of
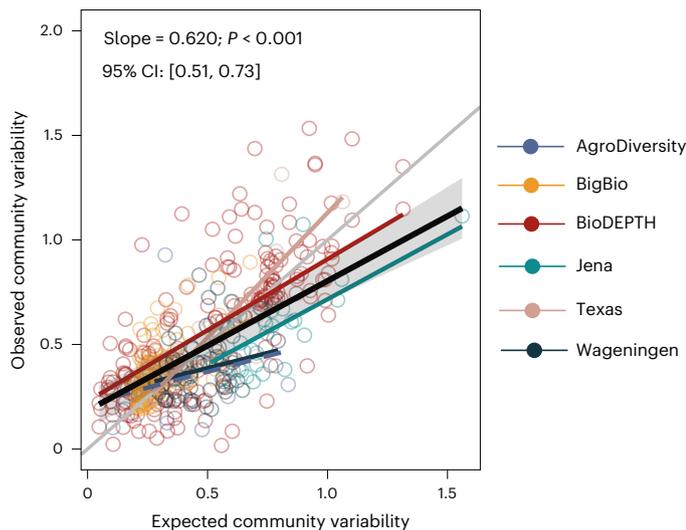
Fig. 5 | The relationship between CV$_{C(O)}$ and CV$_{C(E)}$. The black line with the shaded region represents the overall fit and 95% confidence interval from the linear mixed-effects model across all biodiversity experiments. Coloured lines show the fit within each experiment. Marginal $R^2 = 0.364$, conditional $R^2 = 0.601$. Solid lines show significant, including marginally significant ($P < 0.1$), relationships; dashed lines show non-significant relationships. Two-sided t-tests were used for statistical testing. The grey line represents the 1:1 line.

productivity, or simultaneously decrease them. We note, however, that the exploratory power of above relationships is overall weak, particular for AE$_{SpVar}$, indicating impacts of additional processes.

Discussion

Our study demonstrates that interaction-independent processes, rather than interspecific interactions, mainly account for the stabilizing effects of biodiversity on community biomass production. By using a partitioning framework to disentangle the multiple pathways through which interspecific interactions influence community variability, we show that the desynchronizing effects of interspecific interactions can be offset by their destabilizing effects, resulting in weak NBE$_{CV}$. These findings provide experimental support for predictions from early theoretical studies[9,12,13] and mechanistic insights into empirical observations that interspecific interactions play a weak role in driving the stability of plant communities[17,24,27,32].

Our analyses of both competition models and grassland experiments indicate that the aggregation of species itself, regardless of the strength of their interactions, can generate stabilizing effects on community dynamics because of interspecific variation in temporal fluctuations (Fig. 4). As a result, the variability of ecological communities may be predicted from the variability and synchrony of monoculture dynamics (for example, CV$_{null}$; Fig. 5). In ecological communities, the interaction-independent stabilizing effects can be widespread due to the prevalence of interspecific variation in environmental responses, demographic stochasticity and so on. As species richness increases, the stabilizing effects from interaction-independent processes also strengthen, causing negative associations between species diversity and community variability[11,30,31]. This simple yet broad mechanism provides an explanation for the widely observed positive diversity–stability relationships in observational and experimental studies across systems[33–35].

Despite the negligible net effect of species interactions on community variability, the considerable variance around zero (Fig. 4b) suggests that this effect may vary across contexts such as species combinations[23,36], environmental conditions[15,37] and the duration of the experiment[26,38]. Indeed, our framework disentangles four key pathways through which species interactions affect community variability

(Fig. 2). These pathways include not only the effects of interspecific interactions in shaping average species variability and synchrony, as identified in previous studies[11,27,39], but also two previously overlooked processes: selection for species with higher or lower variability or synchrony. By clarifying these pathways, our framework also enables quantification of their relative contributions to community variability. Our empirical analysis shows a negative AE$_{Syn}$, supporting the hypothesis that competition increases compensatory dynamics among species[11,27]. However, these desynchronizing effects were largely counterbalanced by the concurrent increase in AE$_{SpVar}$, challenging the notion that competition contributes to stabilizing communities through compensatory dynamics[11]. Our empirical analyses also revealed a significant negative selection effect on species variability (Fig. 3), implying that interspecific interactions shift the community towards being dominated by more stable species[36,40]. In grasslands, species with larger biomass and lower variability in monoculture may exhibit competitive advantages in mixtures due to greater efficiencies in acquiring resources such as light and nutrient[41,42]. That said, the selection effects of interspecific interactions on both species variability and synchrony were overall weak in both model and grassland communities (Fig. 4e,f and Extended Data Fig. 2), aligning with the weak roles of selection effects in biodiversity–ecosystem functioning relationships[18,43,44].

Our partitioning framework also provides new opportunities to integrate biodiversity–ecosystem functioning and biodiversity–ecosystem stability relationships, as advocated by recent studies[31,38,45,46]. By comparing the observed community variability with that expected from monocultures, our partitioning framework for biodiversity–stability theory offers a direct parallel to the additive partition framework commonly used in biodiversity–ecosystem functioning studies[18]. Our theoretical and experimental results show that the average and selection effects of interspecific interactions on species variability align with the traditional complementarity and selection effects[18], respectively (Fig. 6 and Extended Data Fig. 3). This may be because species with a greater biomass are often less variable, especially in the presence of demographic stochasticity[41]. This finding supports the hypothesis that the stabilizing effect of biodiversity may be achieved concurrently with enhanced productivity[11,30,47], a conclusion that is not only of theoretical interest but also with practical implications. For instance, a well-designed crop combination that simultaneously achieves higher yields and greater stability would be a major objective of sustainable agriculture[34,48]. That being said, the relationship between biodiversity effects on ecosystem functioning and stability can be more complex when accounting for interaction-independent effects, which contribute to ecosystem stability but not the mean functions. In addition, the biodiversity effects on functioning could strengthen over time, as evidenced by long-term experiments[26]. These complexities may explain the overall weak relationships between biodiversity effects on functioning and stability in our empirical analyses and the mixed relationships between community productivity and stability in recent studies[26,49,50].

Our study fills a long-standing knowledge gap regarding the role of interspecific interactions in shaping ecosystem stability by applying a partitioning framework to community models and grassland experiments. Importantly, our results show that the stabilizing effects of biodiversity largely arise from interaction-independent processes, rather than interspecific interactions. While our experiments involve weeding that may artificially affect interspecific interactions[51,52], the weak net interaction effect is probably not due to weeding, because our analyses did reveal strong interaction effects on the multiple components of ecosystem variability. Our datasets include plant monocultures and mixtures grown under identical conditions, offering an ideal context for deriving the ecological baselines and the various components in our framework. For datasets with experiment units grown in different conditions, such as those encountered in observational field experiments[53], new frameworks will be needed
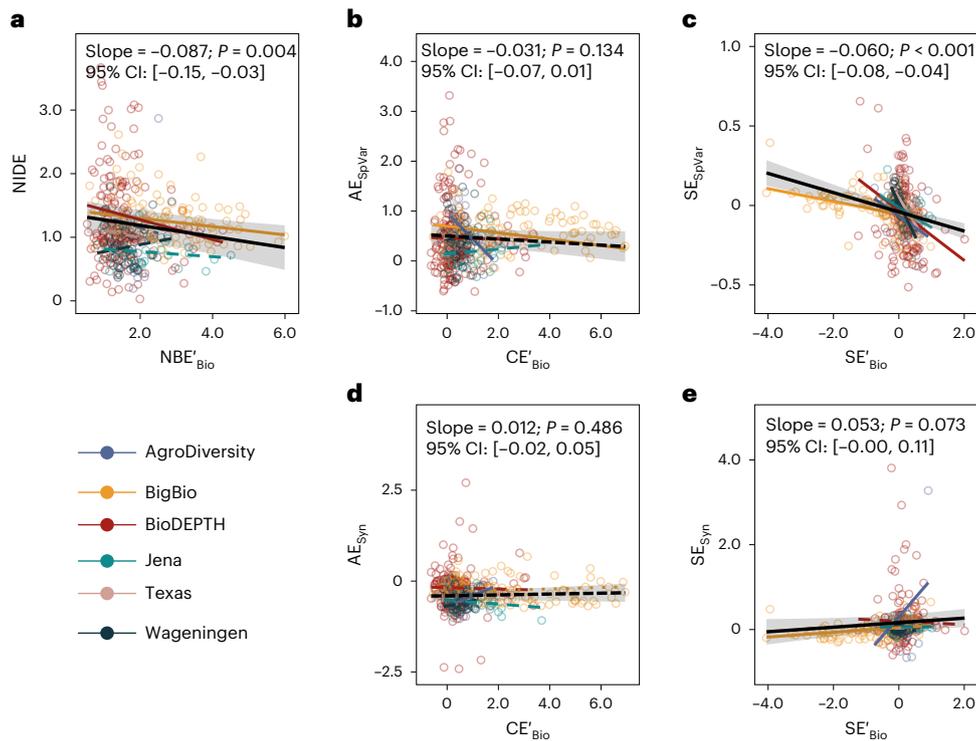
Fig. 6 | Relationships between biodiversity effects on community variability and those on community biomass across grassland biodiversity experiments. **a**, NBE′$_{Bio}$ as a function of NIDE. **b,d**, AE$_{SpVar}$ (**b**) and AE$_{Syn}$ (**d**) as functions of CE′$_{Bio}$. **c,e**, SE$_{SpVar}$ (**c**) and SE$_{Syn}$ (**e**) as functions of SE′$_{Bio}$. Black lines with error bands represent the overall fits and 95% confidence interval from linear mixed-effects models across all biodiversity experiments. Coloured lines show the fit within each experiment. Solid lines show relationships with P values <0.1; dashed lines show non-significant relationships. Two-sided t-tests were used for statistical testing. In **a**, marginal $R^2 = 0.015$, conditional $R^2 = 0.439$; in **b**, marginal $R^2 = 0.007$, conditional $R^2 = 0.346$; in **c**, marginal $R^2 = 0.100$, conditional $R^2 = 0.265$; in **d**, marginal $R^2 = 0.002$, conditional $R^2 = 0.329$; and in **e**, marginal $R^2 = 0.006$, conditional $R^2 = 0.411$.

to construct valid baselines. The partitioning framework developed here opens up research opportunities, including to understand why biodiversity–stability relationships change over time[26,38], how ecosystem stability and its underlying mechanisms respond to global environmental changes (for example, eutrophication[54]), and how more complex species interactions such as facilitation and trophic interactions influence community stability[38,55,56]. Our results shed new light on the mechanisms of biodiversity–ecosystem stability relationships and their intrinsic associations with biodiversity–ecosystem functioning relationships.

Methods

The partitioning framework

We quantify NBE$_{CV}$ as the ratio of CV$_{C(O)}$ to the expected null value (CV$_{null}$), where CV$_{null}$ is the average monoculture variability across component species. To disentangle the contributions of interaction-independent and interaction-dependent effects (NIIE and NIDE, respectively), we constructed a hypothetical community with the same species composition as the focal mixture, where each species maintains its monoculture temporal dynamics (rescaled by species richness; Fig. 1). By taking the variability of this hypothetical community (CV$_{C(E)}$) as the ecological reference, we define NIIE as the ratio of CV$_{C(E)}$ to CV$_{null}$ and NIDE as the ratio of CV$_{C(O)}$ to CV$_{C(E)}$. Therefore: NBE$_{CV} = \frac{CV_{C(O)}}{CV_{null}} = $ NIIE × NIDE (Fig. 1). Our partitioning framework thus requires temporal observational data of species-level functions in both mixtures and monocultures (for example, in biodiversity experiments). Below we explain how we derive NIIE and NIDE, as well as their components, using experimental data.

We denote the biomass of species i at time t in the focal mixture as $X_{i(O)}(t)$ and that in monoculture as $X_{i(M)}(t)$. The biomass of species i in the hypothetical community is defined

as $X_{i(E)}(t) = X_{i(M)}(t) / n$, where n is the number of species in the focal mixture. Let $\mu_{i(Y)} = \text{mean}_t(X_{i(Y)}(t))$ be the temporal mean and $v_{ij(Y)} = \text{cov}_t\left(X_{i(Y)}(t), X_{j(Y)}(t)\right) = \frac{1}{n}\sum_{i,j}\left(X_{i(Y)} - \mu_{i(Y)}\right)\left(X_{j(Y)} - \mu_{j(Y)}\right)$ be the temporal covariance. In these notations, Y denotes observed values from the mixture (O) or monocultures (M), or the expected values from the hypothetical community (E). Community variability by the coefficient of variation of total community biomass is CV$_{C(Y)} = \frac{\sqrt{\sum_{ij} v_{ij(Y)}}}{\sum_i \mu_{i(Y)}}$. The average species variability is defined as CV$_{S(Y)} = \sum_i p_{i(Y)} CV_{i(Y)}$, where $p_{i(Y)} = \frac{\mu_{i(Y)}}{\sum_i \mu_{i(Y)}}$ is the biomass proportion and CV$_{i(Y)} = \frac{\sqrt{v_{ii(Y)}}}{\mu_{i(Y)}}$ is the variability of species i. Species synchrony is defined as: $\varphi_{(Y)} = \frac{\sqrt{\sum_{ij} v_{ij(Y)}}}{\sum_i \sqrt{v_{ii(Y)}}}$ (ref. 39). As such defined[2], we have: CV$_{C(Y)} = $ CV$_{S(Y)} \times \varphi_{(Y)}$. On the basis of these notations, we can obtain NIIE $= \frac{CV_{C(E)}}{CV_{null}}$ and NIDE $= \frac{CV_{C(O)}}{CV_{C(E)}}$, where CV$_{null}$ is the simple mean of monoculture variability, that is, CV$_{null} = \frac{1}{n}\sum_i CV_{i(M)} = \frac{1}{n}\sum_i CV_{i(E)}$. Below we further partition NIIE and NIDE.

The NIIE can be expressed as:

$$\text{NIIE} = \frac{CV_{C(E)}}{CV_{null}} = \underbrace{\frac{n\sum_i CV_{i(E)} p_{i(E)}}{\sum_i CV_{i(E)}}}_{\text{NIIE}_{SpVar}} \times \underbrace{\frac{\sqrt{\sum_{ij} v_{ij(E)}}}{\sum_i \sqrt{v_{ii(E)}}}}_{\text{NIIE}_{Syn}} \quad (4)$$

The first term represents NIIE$_{SpVar}$, which depends on the covariation between the mean and variability of biomass across monocultures. Because CV often decreases with the mean[11], we expect that NIIE$_{SpVar}$ is smaller than 1. The second term represents NIIE$_{Syn}$, which depends on the number of species and the covariation among monocultures.

The NIDE can be re-written as:

$$\text{NIDE} = \frac{CV_{C(O)}}{CV_{C(E)}} = \underbrace{\frac{CV_{S(O)}}{CV_{S(E)}}}_{\text{NIDE}_{\text{SpVar}}} \times \underbrace{\frac{\varphi_{(O)}}{\varphi_{(E)}}}_{\text{NIDE}_{\text{Syn}}} \tag{5}$$

The first term represents $\text{NIDE}_{\text{SpVar}}$, which could be decomposed as (Supplementary Appendix 1):

$$\text{NIDE}_{\text{SpVar}} = \frac{CV_{S(O)}}{CV_{S(E)}} = 1 + \underbrace{\frac{\overline{\Delta CV_i}}{CV_{S(E)}}}_{\text{AE}_{\text{SpVar}}} + \underbrace{\frac{n \times \text{cov}(CV_{i(E)}, \Delta p_i)}{CV_{S(E)}}}_{\text{SE}_{\text{SpVar}}} \tag{6}$$

Here $\Delta p_i = p_{i(O)} - p_{i(E)}$ and $\overline{\Delta CV_i} = \sum_i (\Delta CV_i \times p_{i(O)})$, where $\Delta CV_i = CV_{i(O)} - CV_{i(E)}$. This formula indicates that species interactions can influence species variability by altering the average species variability (referred to as AE_{SpVar}), or via enhancing the dominance of species with higher or lower variability (referred to as SE_{SpVar}). The second term represents NIDE_{Syn}, which could be decomposed as (Supplementary Appendix 1):

$$\text{NIDE}_{\text{Syn}} = \frac{\varphi_{(O)}}{\varphi_{(E)}} = \sqrt{1 + \underbrace{\frac{\overline{\Delta \rho_{ij}}}{\varphi_{(E)}^2}}_{\text{AE}_{\text{Syn}}} + \underbrace{\frac{n^2 \times \text{cov}(\rho_{ij(E)}, \Delta \omega_{ij})}{\varphi_{(E)}^2}}_{\text{SE}_{\text{Syn}}}} \tag{7}$$

Here $\rho_{ij(Y)} = \frac{v_{ij(Y)}}{\sqrt{v_{ii(Y)}}\sqrt{v_{jj(Y)}}}$ and $\omega_{ij(Y)} = \frac{\sqrt{v_{ii(Y)}}\sqrt{v_{jj(Y)}}}{\sum_{ij}\sqrt{v_{ii(Y)}}\sqrt{v_{jj(Y)}}}$, where Y is either E or O and $\overline{\Delta \rho_{ij}} = \sum_{ij}(\rho_{ij(O)} - \rho_{ij(E)})\omega_{ij(O)}$ and $\Delta \omega_{ij} = \omega_{ij(O)} - \omega_{ij(E)}$. This formula indicates that species interaction can influence species synchrony by altering the average species correlation (referred to as AE_{Syn}), or enhancing the dominance of certain pairs of species with higher or lower correlations (referred to as SE_{Syn}). Note that our definition of synchrony involves both intraspecific and interspecific correlations[2,39], thus SE_{Syn} can arise from changes in either interspecific correlations or species unevenness.

Combined, NBE_{CV} could be partitioned multiplicatively into multiple components, that is, $\text{NIIE}_{\text{SpVar}}$ and NIIE_{Syn} and $\text{NIDE}_{\text{SpVar}}$ and NIDE_{Syn}:

$$\text{NBE}_{\text{CV}} = \underbrace{\underbrace{\text{NIIE}_{\text{SpVar}} \times \text{NIIE}_{\text{Syn}}}_{\text{NIIE}} \times \underbrace{\left(1 + \text{AE}_{\text{SpVar}} + \text{SE}_{\text{SpVar}}\right)}_{\text{NIDE}_{\text{SpVar}}} \times \underbrace{\left(1 + \text{AE}_{\text{Syn}} + \text{SE}_{\text{Syn}}\right)^{\frac{1}{2}}}_{\text{NIDE}_{\text{Syn}}}}_{\text{NIDE}} \tag{8}$$

Each component captures how different processes influence community variability relative to monoculture variability, with values greater (smaller) than 1 indicating positive (negative) effects on variability. For $\text{NIDE}_{\text{SpVar}}$ and NIDE_{Syn}, each could be further partitioned additively into one plus average and selection effects of species interactions. Thus, both average (AE) and selection (SE) effects measure the proportional change (in species variability or synchrony) induced by species interactions, with zero values indicating no interaction effect.

Our partitioning framework (equation (8)) mixes additive and multiplicative terms. When applying a logarithmic transformation, the formula becomes:

$$\log(\text{NBE}_{\text{CV}}) = \log(\text{NIIE}_{\text{SpVar}}) + \log(\text{NIIE}_{\text{Syn}}) \\ + \log(\text{NIDE}_{\text{SpVar}}) + \log(\text{NIDE}_{\text{Syn}}) \tag{9}$$

where log represents natural logarithm (logarithm with base e). According to the formula $\log(1 + x) = \sum_{n=1}^{\infty}(-1)^{n+1}\frac{x^n}{n}$, when $|\text{AE}_{\text{SpVar}}|$, $|\text{SE}_{\text{SpVar}}|$, $|\text{AE}_{\text{Syn}}|$ and $|\text{SE}_{\text{Syn}}|$ are small, we can expand $\log(\text{NIDE}_{\text{SpVar}})$ and $\log(\text{NIDE}_{\text{Syn}})$ as follows:

$$\log(\text{NIDE}_{\text{SpVar}}) = \sum_{n=1}^{\infty}(-1)^{n+1}\frac{(\text{AE}_{\text{SpVar}} + \text{SE}_{\text{SpVar}})^n}{n} \tag{10}$$

$$\log(\text{NIDE}_{\text{Syn}}) = \frac{1}{2}\sum_{n=1}^{\infty}(-1)^{n+1}\frac{(\text{AE}_{\text{Syn}} + \text{SE}_{\text{Syn}})^n}{n} \tag{11}$$

In our study (Figs. 3 and 4), we used two-order approximations without the interaction term, that is,

$$\log(\text{NIDE}_{\text{SpVar}}) \approx \underbrace{\left(\text{AE}_{\text{SpVar}} + \frac{\text{AE}_{\text{SpVar}}^2}{2}\right)}_{\text{AE}_{\text{SpVar}}^{\text{T}}} + \underbrace{\left(\text{SE}_{\text{SpVar}} + \frac{\text{SE}_{\text{SpVar}}^2}{2}\right)}_{\text{SE}_{\text{SpVar}}^{\text{T}}} \tag{12}$$

$$\log(\text{NIDE}_{\text{Syn}}) \approx \underbrace{\left(\frac{\text{AE}_{\text{Syn}}}{2} + \frac{\text{AE}_{\text{Syn}}^2}{4}\right)}_{\text{AE}_{\text{Syn}}^{\text{T}}} + \underbrace{\left(\frac{\text{SE}_{\text{Syn}}}{2} + \frac{\text{SE}_{\text{Syn}}^2}{4}\right)}_{\text{SE}_{\text{Syn}}^{\text{T}}} \tag{13}$$

Here $\text{AE}_{\text{SpVar}}^{\text{T}}$ represents the log-scaled approximation of effects of AE_{SpVar}, and similarly for $\text{SE}_{\text{SpVar}}^{\text{T}}$, $\text{AE}_{\text{Syn}}^{\text{T}}$ and $\text{SE}_{\text{Syn}}^{\text{T}}$. Under these approximations, we can express $\log(\text{NBE}_{\text{CV}})$ as a number of additive terms:

$$\log(\text{NBE}_{\text{CV}}) \approx \log(\text{NIIE}_{\text{SpVar}}) + \log(\text{NIIE}_{\text{Syn}}) \\ + \left(\text{AE}_{\text{SpVar}}^{\text{T}} + \text{SE}_{\text{SpVar}}^{\text{T}}\right) + \left(\text{AE}_{\text{Syn}}^{\text{T}} + \text{SE}_{\text{Syn}}^{\text{T}}\right) \tag{14}$$

We note that these approximations hold only for small values of $|\text{AE}_{\text{SpVar}}|$, $|\text{SE}_{\text{SpVar}}|$, $|\text{AE}_{\text{Syn}}|$ and $|\text{SE}_{\text{Syn}}|$; in general cases, higher-order and interaction terms need to be considered. The natural-scale results of the average effect and the select effect in this study are shown in Supplementary Figs. 2 and 3.

Linking biodiversity effects on ecosystem functioning and stability

Our partitioning framework for biodiversity effects on ecosystem stability aligns conceptually with the classic additive partition for biodiversity effects on ecosystem functioning[20]. In this context, ref. 20 originally defined NBE_{Bio} as the difference between the observed mixture biomass (B_O) and the expected value from monoculture biomass (B_E), and they partitioned it additively into complementarity (CE_{Bio}) and selection (SE_{Bio}) effects, that is, $\text{NBE}_{\text{Bio}} = B_O - B_E = \text{CE}_{\text{Bio}} + \text{SE}_{\text{Bio}}$. To see the link of this framework to ours, we used an alternative definition of net biodiversity effect by the ratio of mixture and monoculture biomass and rewrote it as follows:

$$\text{NBE}'_{\text{Bio}} = \frac{B_O}{B_E} = 1 + \frac{\text{NBE}_{\text{Bio}}}{B_E} = 1 + \frac{\text{CE}_{\text{Bio}}}{B_E} + \frac{\text{SE}_{\text{Bio}}}{B_E} = 1 + \text{CE}'_{\text{Bio}} + \text{SE}'_{\text{Bio}} \tag{15}$$

where $\text{CE}'_{\text{Bio}} \triangleq \text{CE}_{\text{Bio}}/B_E$ and $\text{SE}'_{\text{Bio}} \triangleq \text{SE}_{\text{Bio}}/B_E$ represent the proportional changes in mixture biomass driven by complementarity and selection effects, respectively. This reformulation facilitates comparisons of the complementarity and selection effects in biodiversity–ecosystem functioning (in relative forms, that is, CE' and SE') with the average and selection effects in biodiversity effects on community variability (that is, AE and SE terms in equation (8)).

Theoretical models

We use a discrete-time Lotka–Volterra model where population dynamics are governed by competition and environmental and demographic stochasticity[13]:

$$N_i(t+1) = N_i(t)\exp\left(r_i\left[1 - \frac{N_i(t)}{K_i} - \sum_{i \neq j}\frac{\alpha_{ij}N_j(t)}{K_i}\right] \\ + v_{e,i}\mu_{e,i}(t) + \frac{v_{d,i}\mu_{d,i}(t)}{\sqrt{N_i(t)}}\right) \tag{16}$$

where $N_i(t)$ is the biomass of species i at time t; r_i and K_i are the intrinsic growth rate and carrying capacity of species i, respectively. Parameter α_{ij} is a competition coefficient describing the per capita effect of species j on the growth rate of species i. Thus, the dynamics of monoculture could be simulated by setting $\alpha_{E,ij} = 0$ and $K_{E,i} = \frac{1}{n}K_i$ (n is the number of

observed/mixed community). The term $v_{e,i}\mu_{e,i}(t)$ represents species-specific responses to the environmental stochasticity, where $v_{e,i}$ denotes the environmental variance and $\mu_{e,i}(t)$ represents a normal random variable with zero mean and unit variance that are independent through time (that is, white noise). The term $\frac{v_{d,i}\mu_{d,i}(t)}{\sqrt{N_i(t)}}$ represents the effect of demographic stochasticity, where $v_{d,i}$ denotes the demographic variance and $\mu_{d,i}(t)$ is a normal random variable with zero mean and unit variance that are independent through time. Following ref. 57, we assume that the effect of demographic stochasticity scales with population size ($N_i(t)$).

With the above model, we first consider a symmetric case: $r_i = r$, $K_i = K$, $\alpha_{ij} = \alpha$, $v_{e,i} = \sigma_e$, $v_d = 0$ and the environmental noises are independent across species, under which we can obtain the solutions for the various components of biodiversity effects:

$$\text{NIIE}_{\text{Syn}} = \sqrt{\frac{1}{n}} \tag{17}$$

$$\text{NIIE}_{\text{SpVar}} = 1 \tag{18}$$

$$\text{AE}_{\text{SpVar}} = \sqrt{\frac{1+(n-1)\theta}{n}} - 1 \tag{19}$$

$$\text{AE}_{\text{Syn}} = \frac{n}{1+(n-1)\theta} - 1 \tag{20}$$

$$\text{SE}_{\text{SpVar}} = \text{SE}_{\text{Syn}} = 0 \tag{21}$$

where $\theta = \frac{r(2-r)}{\frac{(1-\alpha)r}{1+(n-1)\alpha}\left(2-\frac{(1-\alpha)r}{1+(n-1)\alpha}\right)}$. When $r < 1$, θ increases as competition strength α increases, thus AE_{SpVar} increases with α and AE_{Syn} decreases with α. When $r > 1$, the patterns are more complex[39]. On the basis of equations (17)–(21), we have:

$$\text{NIIE} = \underbrace{1}_{\text{NIIE}_{\text{SpVar}}} \times \underbrace{\left(\frac{1}{n}\right)^{\frac{1}{2}}}_{\text{NIIE}_{\text{Syn}}} = \sqrt{\frac{1}{n}} \tag{22}$$

$$\text{NIDE} = \underbrace{\left(1 + \underbrace{\sqrt{\frac{1+(n-1)\theta}{n}} - 1}_{\text{AE}_{\text{SpVar}}} + \underbrace{0}_{\text{SE}_{\text{SpVar}}}\right)}_{\text{NIDE}_{\text{SpVar}}} \times \underbrace{\left(1 + \underbrace{\frac{n}{1+(n-1)\theta} - 1}_{\text{AE}_{\text{Syn}}} + \underbrace{0}_{\text{SE}_{\text{Syn}}}\right)^{\frac{1}{2}}}_{\text{NIDE}_{\text{Syn}}} = 1 \tag{23}$$

These solutions demonstrate that, when all species compete in a symmetric manner, there is no selection effect on either species variability or synchrony because symmetric competition do not favour any specific species. On the other hand, species competition inflates population fluctuations in compensatory manners, resulting in increased average species variability but decreased species synchrony[12,13]. Thus, in this competition model species interactions influence community variability through positive average effects on species variability and negative average effects on synchrony. These two average effects have exactly the same magnitudes, regardless of the strength of species interaction, resulting in no net interaction-dependent effect (NIDE = 1).

To explore the effect of species richness and interaction (competition in this model) on the relative contributions of the various mechanisms underlying the stabilizing effect of biodiversity, we simulated communities with species richness (n) ranging from 2 to 10 with the following parameters: $\alpha_{ij} = U(0.01,0.41)$, $\log_2(r) \sim U(-1,0)$, $\log_2(K) \sim U(-1,0)$, $\mu_{ei} = 0.2$, $\mu_{di} = 0.1$ and v_{di} and $v_{ei} \sim U(0.0,0.1)$. We omitted simulated communities where at least one species went extinct and retained 10,000 replicates of coexisting communities for each richness level. Community variability was calculated on the basis of the final 100

time steps of each replicate (overall 1,000 steps for each replicate). For each community, we also simulated the dynamics of monocultures for all constituent species using equation (16).

On the basis of the simulated dynamics of monocultures and multispecies communities, we calculated the various components of our partitioning framework (Fig. 2). We examine how these components change with species richness and competition strengths and test their relationships with the CE'_{Bio} and SE'_{Bio} effects on community biomass.

Empirical analysis

Our empirical analyses were based on a dataset consisting of 34 biodiversity experiments across North America and Europe[3]. These experiments were initially designed to test the relationship between biodiversity and ecosystem functioning by manipulating species richness. The monoculture treatments serve as references to assess the effect of species interactions underlying the stabilizing effects of diversity. We excluded multispecies plots that lacked monocultures of any constituent species. While our framework could be easily adapted to tackle uneven initial proportions, we excluded experiments with uneven initial abundances to avoid additional confounding factors across experiments in the present study. For Agrodiversity experiments, we consider only the high-density treatment to match the experimental design of other studies; also, plots with the same species composition (though different initial proportions) are considered as the same experiment treatment. Our dataset comprises observation from 447 plots with species richness ranging from 2 to 16 and temporal observations from 3 to 18 years. Detailed descriptions of these experiments can be found in Supplementary Table 1.

With these experiments and our partitioning framework, we calculated the different components underlying biodiversity effects on community variability and examined how they changed with species richness using linear mixed-effects models. We also used random-effects models to test whether the overall mean of each component across all studies differed from zero. In these models we used a nested random effect (study/experiment), since some experiments have been collectively designed and analysed in previous studies, such as the BioDEPTH[58] and the Agrodiversity Experiment network[59]. We further tested the relationship between biodiversity effects on community biomass and variability under given species richness, where the nested structure of random effect is adapted to study/experiment/sown plant richness. We then tested the relationship between expected community variability and observed community variability using this linear mixed-effects model. In these analyses, we applied a log-transformation to NIIE and the net interaction-dependent effect on population variability ($\text{NIDE}_{\text{SpVar}}$) and synchrony ($\text{NIDE}_{\text{Syn}}$) making them additive for all analyses. The effect of biodiversity on community biomass is determined and partitioned through equation (5). All statistical analyses are performed by nlme package in R v.4.2.2.

Reporting summary

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

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Acknowledgements

Author contributions

S.W. and B.M. designed the study. B.M., M. Luo and S.W. performed the research. S.W. developed the partitioning framework, with help from B.M., M. Luo and M. Loreau. B.M. and M. Luo performed theoretical analyses. B.M. conducted empirical analyses. D.C., N.E., B.W., J.v.R. and F.I. contributed experiment data. B.M. and S.W. wrote the first draft. M. Loreau, P.H., D.C., N.E., D.R., B.W., L.Z., M. Liang, J.v.R. and F.I. contributed substantially to the revision of the paper.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-025-02787-4.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-025-02787-4.

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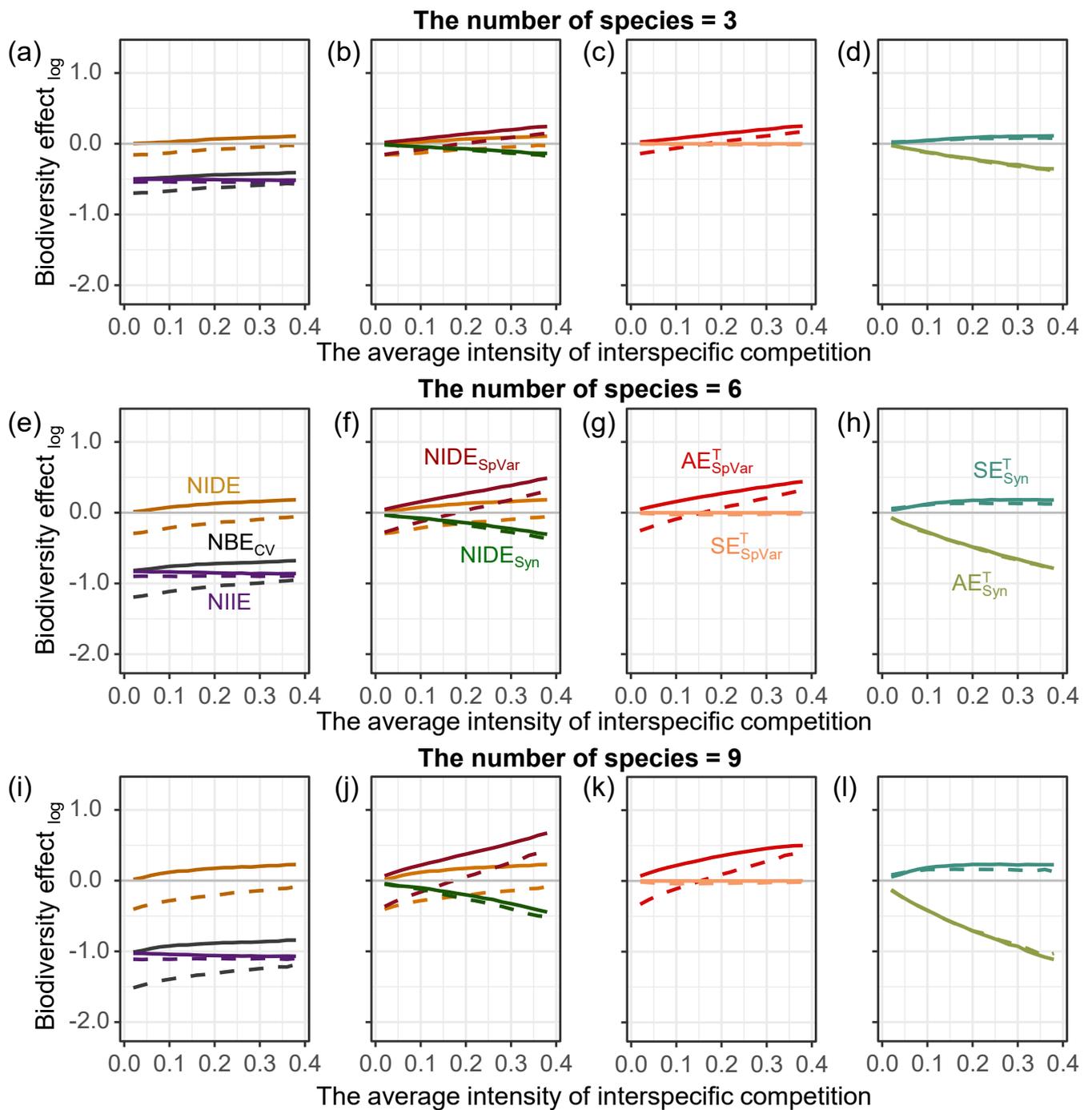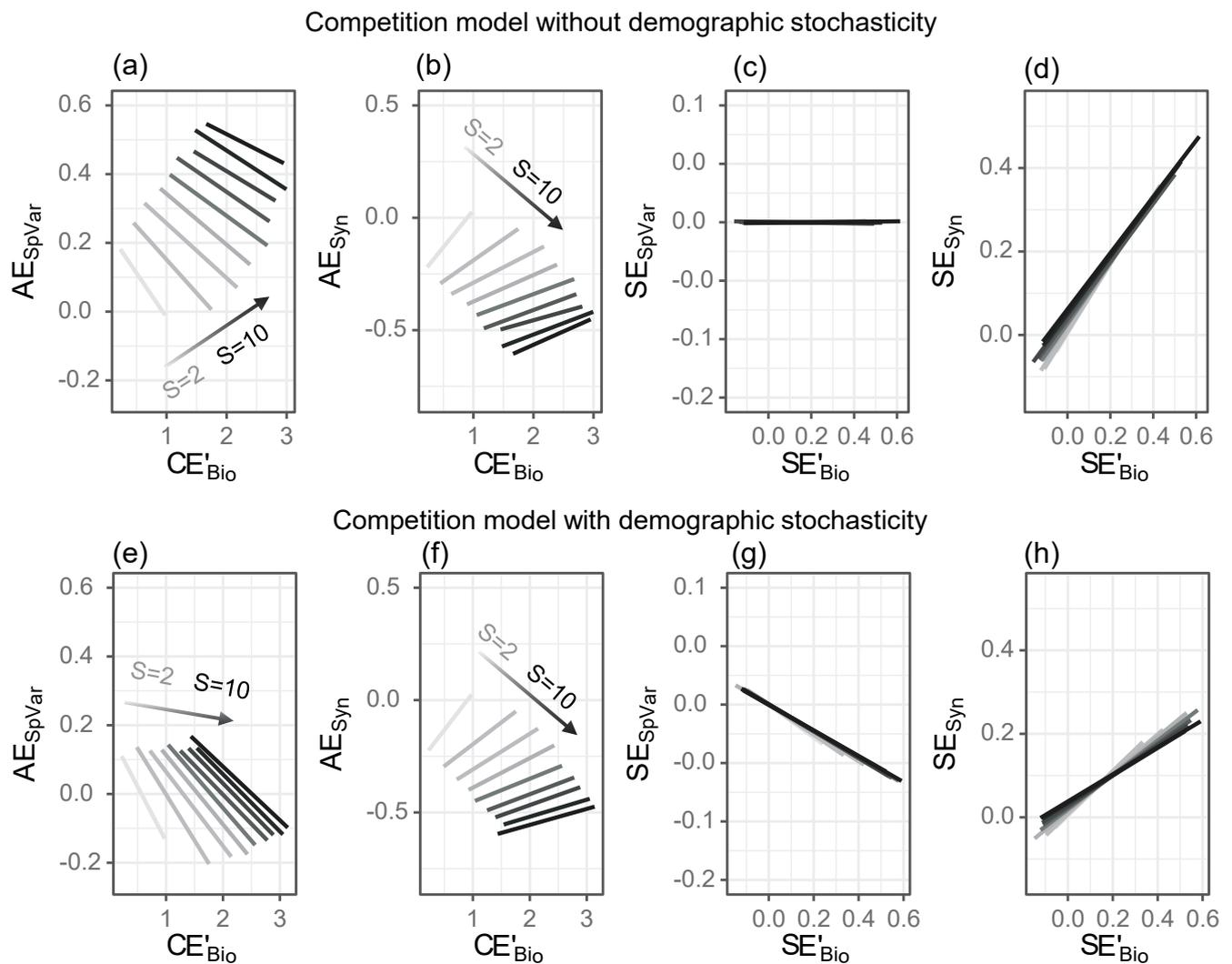
Extended Data Fig. 1 | Relationships between the strength of interspecific competition and the multiple components underlying biodiversity effects on community variability in the competition model. (**a-d**) across 3-species communities; (**e-h**) across 6-species communities; and (**i-l**) across 9-species communities. Colored lines represent least squares fits across 3,000 simulated communities at equilibrium (observational length = 100). Parameters are $\alpha_{ij} = U(0.01, 0.01 + 2\bar{\alpha})$, $\log_2(r) \sim U(-1, 0)$, $\log_2(K) \sim U(-1, 0)$, $\mu_{e,i} = 0.2$ and $v_{e,i} = U(0, 0.1)$. Solid lines represent scenarios without demographic stochasticity ($\mu_{d,i} = 0$), and dashed lines with demographic stochasticity ($\mu_{d,i} = 0.1$ and $v_{d,i} = U(0, 0.1)$).
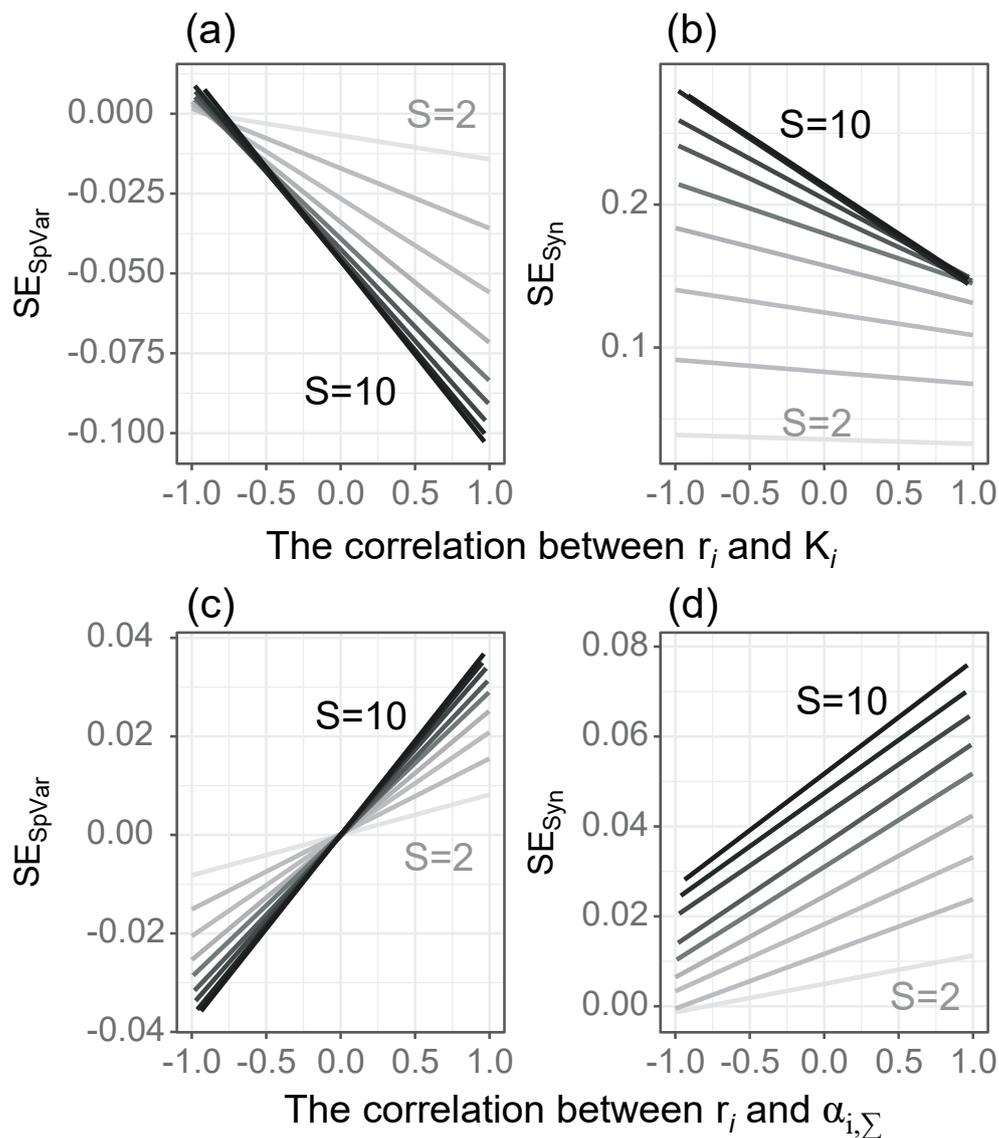
Extended Data Fig. 2 | Selection effects of interspecific interaction on species variability (SE$_{SpVar}$) and synchrony (SE$_{Syn}$) change with scenarios of parameters in a competition model. (**a**) SE$_{SpVar}$ and (**b**) SE$_{Syn}$ as functions of the correlation between r and K. Parameters are: $\alpha_{ij} = 0.2$, $\log_2(r)$-U(-1, 0), $\log_2(K)$ - U(-1, 1), $\mu_{e,i} = 0.2$, $\mu_{d,i} = 0.1$ both $\nu_{d,i} = \nu_{e,i} = 0.05$. (**c**) SE$_{SpVar}$ and (**d**) SE$_{Syn}$ as functions of the correlation between r and $\alpha_{i,\Sigma}$ (that is, the overall competition strength species i receives from other species). Parameters are: $\alpha_{ij} = $ U(0.01, 0.41), $\alpha_{ji} = 0.42 \cdot \alpha_{ij}$, $\log_2(r)$-U(-1, 0), $\log_2(K) = 0$, $\mu_{e,i} = 0.2$, $\mu_{d,i} = 0.1$ both $\nu_{d,i} = \nu_{e,i} = 0.05$. Lines represent least-square fits under respective scenarios, fitted across 10000 simulated communities at equilibrium (length = 100). The black lines range from dark to light represent different levels of species richness (S = 2, ..., 10).

Extended Data Fig. 3 | Relationship between components from the partitioning framework for ecosystem functioning (that is, CE$'_{Bio}$, SE$'_{Bio}$) and those from our partitioning framework for ecosystem variability. (**a-d**) Relationships from competition models without demographic stochasticity. Parameters are α_{ij} = U(0.01, 0.41), $\log_2(r)$ ~ U(-1, 0), $\log_2(K)$ ~ U(-1, 0), $\mu_{e,i}$ = 0.2, $\mu_{d,i}$ = 0, and $\nu_{e,i}$ = U(0.0, 0.1). (**e-h**) Relationships from competition models with demographic stochasticity. In this case, $\mu_{d,i}$ = 0.1, and $\nu_{d,i}$ = U(0.0, 0.1). Lines represent least-square fits under respective scenarios, fitted across 10000 simulated communities at equilibrium (length = 100). The black lines range from dark to light represent different levels of species richness (S = 2, …, 10).

(a) Competition model without demographic stochasticity

(b) Competition model with demographic stochasticity

Extended Data Fig. 4 | Relationship between net biodiversity effect in ecosystem functioning (NBE'$_{Bio}$) and the net interaction-dependent effect on community variability (NIDE) across simulated communities.
(**a**) Relationships from competition models without demographic stochasticity. Parameters are $\alpha_{ij} = U(0.01, 0.41)$, $\log_2(r) \sim U(-1, 0)$, $\log_2(K) \sim U(-1, 0)$, $\mu_{e,i} = 0.2$,

$\mu_{d,i} = 0$, and $v_{e,i} = U(0.0, 0.1)$. (**b**) Relationships from competition models with demographic stochasticity. In this case, $\mu_{d,i} = 0.1$, and $v_{d,i} = U(0.0, 0.1)$. Lines represent least-square fits under respective scenarios, fitted across 10000 simulated communities at equilibrium (length = 100). The black lines range from dark to light represent different levels of species richness treatment (S = 2, ..., 10).
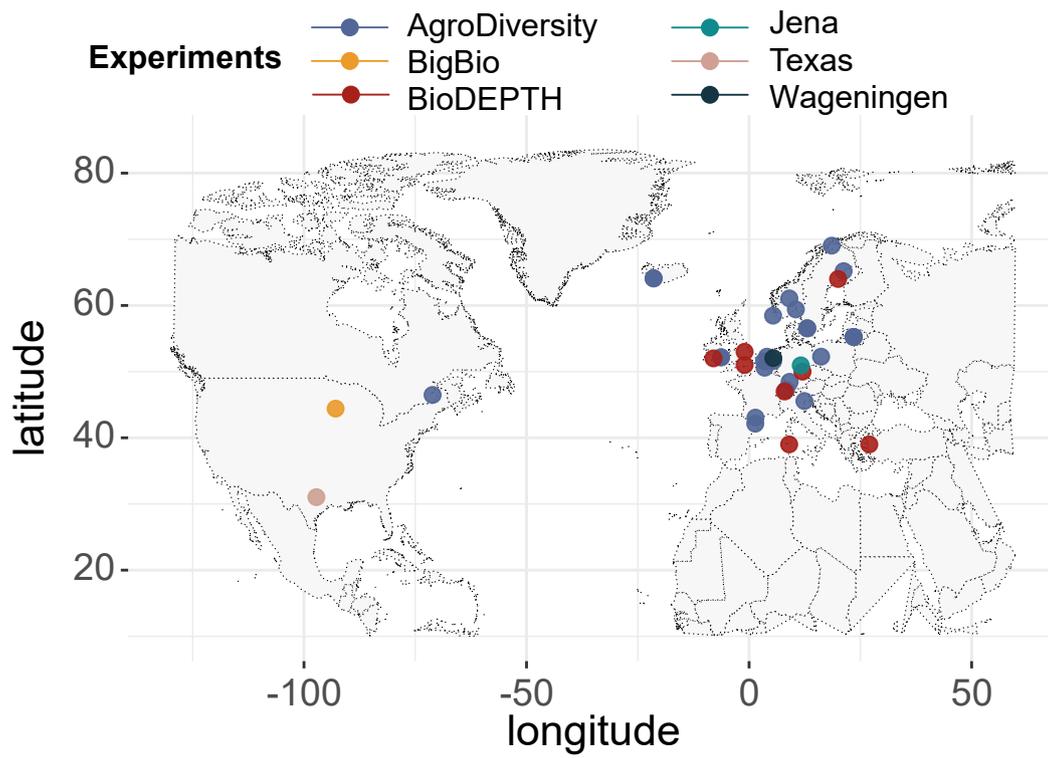
Extended Data Fig. 5 | Locations of the grassland biodiversity experiments. Dots with the same colour represent experiments belonging to the same research network.

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☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
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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	N/A
Data analysis	All analyses were performed in R 4.2.2 run via RStudio. We used a linear mixed-effects model (LMM) where study/experiment were included as a nested random effect using "nlme" packages (V3.1).

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 original data sets used in this study are available from data repositories of included studies, or upon request to data owners. The detailed information of included studies was documented on Table S1.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

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
Ethics oversight	N/A

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We develop a new partitioning framework to disentangle the effects of inter-specific interactions on ecosystem variability from those of interaction-independent processes. We then apply this framework to competition models and a dataset of grassland biodiversity experiments to quantify the multiple processes underlying biodiversity-variability relationship.
Research sample	Our dataset includes 34 biodiversity experiments conducted across North America and Europe. These experiments were originally designed to investigate the relationship between biodiversity and ecosystem functioning. Each experiment involved the manipulation of plant species richness in a grassland setting and collected aboveground plant biomass annually for at least three years.
Sampling strategy	Our dataset consists of temporal observations from 447 plots, with species richness ranging from 2 to 16. All experiments include monoculture treatments as reference points to evaluate the role of species interactions in driving the stabilizing effects of diversity.
Data collection	Not applicable. All raw data was provided by the original owners to the corresponding author and then harmonized across datasets for analysis by the first author.
Timing and spatial scale	The temporal observations in our dataset span from 3 to 18 years across different experiment sites.
Data exclusions	We excluded mixture plots that included at least one species without monoculture treatments, because our theoretical framework require monocultures of all constituent species. We also excluded experiments with uneven initial abundances. Although our framework could be easily adapted to tackle uneven initial proportions, we excluded them in the present study to avoid additional confounding factors across experiments.
Reproducibility	To increase transparency and reproducibility, the codes used for data preparation and analyses is available in github (https://github.com/kklm500/NATECOLEVOL-25010167.git).
Randomization	The experiments in our dataset assigned plot locations and determined the composition of multi-species communities randomly.
Blinding	Not applicable to our study.

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

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

Methods

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

Plants

Seed stocks	Not applicable to our study.
Novel plant genotypes	Not applicable to our study.
Authentication	Not applicable to our study.